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GRASSLAND VEGETATION IN THE BIG HORN MOUNTAINS, WYOMING

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Grasslands cover approximately one-third of the 1.1 million acres within the Bighorn National Forest in north-central Wyoming. Most of the remaining area is forested. Grasslands are even more extensive in the Big Horn Mountains at the lower elevations, where climate does not favor the development of forests. These mountain grasslands have furnished summer grazing to range livestock since the 1880's. Jack (1900), describing the livestock operations on the Bighorn National Forest and adjacent ranges, mentioned that large areas were intensively used by sheep, although cattle also were grazed.

The grasslands have continued to be an important range resource to the local livestock economy. In addition to their direct contribution to the range livestock industry, mountain grasslands and intermingled forested areas have supplied water, forest products, habitat for game, and recreation. These contributions have been recognized and prized for many years.

There is no quantitative description of the vegetation before the range was grazed by domestic livestock; however, there are some accounts of the vegetation, geology, and soils. Darton's monograph (1906) thoroughly treats the geology of the area and Love et al. (1955) supplement this work. Darton mentions gross points about the vegetation but generally in a cursory manner. Jack (1900) discusses the general appearance of the vegetation and the relative importance of some species as forage plants for cattle and sheep. General soil characteristics are described by Thorp et al. (1939) and Dunnewald et al. (1939), and details on organic matter, phosphorous content, and timber-grassland soil characteristics are reported by Dunnewald (1929, 1930). Other references to some earlier accounts of the vegetation and impressions of the area are cited by Hurd and Kissinger (1952).

Recent work in this area has contributed quantitative information, particularly on the herbaceous vegetation and its management. In a preliminary report Hurd and Kissinger (1952) presented data on composition and production of vegetation, growth and development of several grasses, and preference and use of the vegetation by livestock. Beetle (1956) recognized a difference in vegetative patterns within this area and between this and adjacent areas. He presented a modified list of species and the estimated cover for the most common ones. Generally, his estimates of cover pertain to ranges currently being grazed by either cattle or sheep. He also described and interpreted the influence of past use by livestock and game upon the vegetation.

This report provides quantitative information to aid in the more intensive management of these and similar ranges. Results are presented from inventories of grassland stands in the 7,000-8,500 ft elevation zone which has been grazed by cattle for many years and is commonly called "cattle range."

METHODS

The original objective was to examine and inventory stands that had never been grazed by domestic livestock but represented site conditions commonly found on cattle range. Widespread grazing made modification necessary. The 9 stands selected fell into 3 categories: (a) never grazed by domestic livestock, (b) lightly grazed by cattle and horses for the past 30 yr or longer, and (c) formerly grazed but now completely protected from livestock grazing. Although additional livestock exclosures were present, they generally were believed to be too recent or otherwise inadequate to give a representative picture of the site potential. Included in this category

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TABLE I. Site characteristics of 9 grassland stands, Bighorn National Forest, Wyoming

Stand	Elevation	Approximate annual precipitation	Per cent slope and aspect	Length of protection[1]	Size	Underlying rock	
	(feet)	(inches)		(years)	(acres)		
1	7,000	20	9 NE	(2)	10	Sandstone Shale	Surface soils 2-6 in. thick, dark brown silt loam neutral to slightly acid. Subsoils about 20 in. thick, red to yellowish-brown clay loams or clays neutral to slightly alkaline at lower depths. Rocks common in stands 2 and 3, increasing in depth in all stands. Stand 2, a gentle ridge with limestone rocks on surface.
2	7,000	20	3 NW	(2)	3	Limestone	
3	7,000	20	9 W	(2)	8	Limestone	
4	8,100	26	17 N	15	0.5	Shale Sandstone	Surface soils 6-11 in. thick, very dark brown silt loams slightly to moderately acid. Sub-soils about 25-30 in. thick, brown to grayish-brown clay loams or clays. Calcareous at lower depths with a pH of 8.0. Moisture relations favorable and fertility levels high.
5	8,000	26	8 SSE	30	10	Shale Sandstone	
6	8,400	26	2 E	30	20	Limestone	
7	7,400	19	13 N	15	1	Granite	Surface soils 4-6 in. thick, dark brown, moderately acid, gravelly sandy loams. Subsoils about 15-20 in. thick with a coarse gravelly loam texture, brown to yellow-brown and moderately acid having a pH of 5.1.
8	8,000	20	2 W	5	3	Granitic-sedimentary drift	
9	8,200	21	3 W	10	1	Granitic-sedimentary drift	

[1] Includes years of light grazing on stands 5 and 6.
[2] Never grazed by domestic livestock.

were all exclosures on sites dominated by big sagebrush (*Artemisia tridentata*)[2]. General site characteristics for the 9 selected stands are in Table I. All stands were accessible to deer and elk.

The point quadrat method was used to obtain cover data. The equipment consisted of a 2 in. × 2 in. meter-long oak bar supported at each end by a metal frame. Holes one decimeter apart were bored through the oak piece. Pins were made from 1/16 in. welding rod sharpened to a point. The frame was set up at 5 different places inside each meter-square plot, and there were 10 such plots systematically distributed in the stand. Distribution of points within a square meter can be visualized as occurring at the corners of every 10 cm × 20 cm rectangle inside the square meter frame. Thus, there were 50 point locations identified within each square-meter plot, or 500 points for the entire stand.

Point contacts were recorded in 2 ways. The first thing the point hit as it descended toward the ground was recorded as a "crown" contact because generally this was the aerial part of a plant. After the crown contact had been recorded the pin was lowered until it struck a plant base, litter, rock, or bare soil; this was called a "basal" contact. Sometimes the first contact was a plant base, litter, rock, or bare ground. If so, this contact was recorded both as a crown and basal contact. Thus there were always 50 crown and 50 basal contacts within each square-meter plot.

An inventory was made of each square-meter plot and those species not recorded by the point quadrat method were listed. This inventory was the basis for determining the frequency percentage of each species in every stand and these values were averaged for the 9 stands. Constancy percentages by species also were based on the square meter plot inventories.

Specimens of most of the species on the sample plots are deposited at the Rocky Mountain Herbarium, University of Wyoming, at Laramie. C. L. Porter, curator, aided in identifying the specimens.

Ground cover was determined by dividing contacts, both crown and basal, for the various categories of cover by the total number of contacts (500) for the stand. The quotient was multiplied by 100 to give the percentage. Vegetal com-

[2] Except where author's name is given nomenclature follows Harrington (1954).

position by individual species within a stand was determined by dividing total crown contacts for each species by the total crown contacts for all vegetation and multiplying by 100 to give the percentage. The same procedure was used to get species composition for basal contacts.

Herbage production was obtained in 1955 by clipping ten 2 ft × 2 ft plots systematically distributed in each stand. Species or groups of species determined from previous estimates to be prominent were clipped separately. The remaining vegetation was then clipped and segregated into "other grasses and sedges" and "other forbs." Green weights were recorded to the nearest gram. Samples of all species or groups were air-dried and used to convert green to air-dry weights.

Grazed areas contiguous to 6 of the 9 selected stands were examined. On these sites only basal contact was recorded. Here, as well as in the 9 selected stands, the point quadrat inventories generally were made both in 1954 and 1955 and approximately at the peak of maximum cover development. Data for the two years were averaged.

Results

All 9 stands were similar in that vegetation and litter covered most of the ground surface, and bare soil and rock were generally in small amounts. When crown contacts were used as the basis for analyzing ground cover of the 9 stands the averages for the components were: vegetation 82.0%, litter 16.1%, bare soil 1.7%, and rock 0.2%. Vegetation ranged from 65.2-91.0%. A lower percentage of vegetation in a stand invariably meant a higher percentage of litter because in no stand did bare soil plus rock exceed 5.2% of the ground cover. When basal contacts were used to analyze the ground cover the average percentage of the ground cover components were: vegetation 16.7, litter 80.2, bare soil 2.9, and rock 0.2. With this base, the percentage vegetation ranged from 9.0-24.2%. Again, a smaller amount of vegetation in a stand meant a greater amount of litter with little change in bare soil and rock.

Vegetal Composition

Grasses and sedges made up about 65% of the vegetal cover, although there was considerable variation among the stands (Table II). Forbs accounted for the bulk of the remaining cover. Of the 90 species present, 28 (31%) were grasses and sedges, and 60 (67%) were forbs. Rose (*Rosa* spp.) and selaginella (*Selaginella densa*) completed the list. Since stand inventories were made usually in August, some of the early flower-

Table II. Average cover, frequency, and constancy percentages for each species in 9 stands

Species	Cover		Frequency	Constancy
	C[1]	B[2]		
	%	%	%	%
Agropyron albicans	0.2	0.3	7	33.3
Agropyron dasystachyum	2.6	2.0	66	100.0
Agropyron spicatum	.6	.5	14	22.2
Agropyron subsecundum	.6	.7	18	66.7
Agropyron trachycaulum	2.7	3.1	41	77.8
Agrostis scabra	.6	.3	18	66.7
Bromus anomalus	(3)	0	1	11.1
Bromus pumpellianus	3.9	3.3	39	55.6
Calamagrostis purpurascens	0	0	2	22.2
Carex elynoides	.1	.2	1	11.1
Carex obtusata	7.8	11.2	97	100.0
Carex petasata	0	0	7	22.2
Carex phaeocephala	.8	.4	14	77.8
Carex podocarpa	(3)	0	1	11.1
Danthonia intermedia	.7	1.1	11	55.6
Festuca idahoensis	25.1	22.6	97	100.0
Hesperochloa kingii	3.5	5.1	28	66.7
Juncus balticus	0	0	1	11.1
Koeleria cristata	2.7	3.5	84	100.0
Muhlenbergia richardsonis	.7	1.0	14	22.2
Melica spectabilis	.1	0	3	11.1
Poa ampla/canbyi	1.1	1.3	0	0
Poa cusickii	1.0	.8	26	44.4
Poa interior	1.3	1.4	24	66.7
Poa pratensis	.1	.3	7	22.2
Poa secunda	3.1	3.1	49	77.8
Stipa columbiana	4.0	5.2	38	55.6
Total grasses and sedges	63.3	67.4		
Achillea lanulosa	2.4	2.2	65	100.0
Agoseris glauca	4.0	3.6	74	100.0
Allium brevistylum	.2	.1	9	33.3
Allium schoenoprasum	.1	.2	9	22.2
Antennaria anaphaloides	.1	.3	14	33.3
Antennaria rosea	.4	.1	34	66.7
Arabis drummondii	(3)	0	4	22.2
Arabis nuttallii	(3)	.1	33	55.6
Arenaria congesta	.7	1.7	57	100.0
Arnica fulgens	.3	.6	30	66.7
Artemisia frigida	.1	.1	12	22.2
Artemisia ludoviciana	0	0	1	11.1
Aster foliaceus	.4	.3	32	44.4
Astragalus spp.	1.1	0	25	33.3
Balsamorhiza incana	.5	.2	15	55.6
Besseya cinera	.1	0	10	11.1
Calochortus gunnisonii	(3)	0	4	33.3
Campanula rotundifolia	.5	.6	51	100.0
Castilleja lutea	0	0	1	11.1
Cerastium arvense	1.5	1.7	99	100.0
Chrysopsis villosa	1.1	.2	24	33.3
Clematis hirsutissima	.1	0	3	22.2
Collomia linearis	.3	.3	9	33.3
Delphinium bicolor	.1	0	4	33.3
Dodecatheon conjugens	0	.1	3	11.1
Erigeron compositus	(3)	.2	7	11.1
Erigeron gracilis	.3	.3	13	33.3
Erigeron subtrinervis	.8	0	26	55.6
Erigeron ursinus	0	0	3	11.1
Eriogonum subalpinum	.3	0	14	55.6
Fragaria spp.	.1	0	10	22.2
Gxillardia aristata	0	0	1	11.1
Galium boreale	2.4	1.3	72	88.9
Gentiana forwoodii	(3)	.1	2	11.1
Geranium viscosissimum	.2	.1	13	22.2
Geum ciliatum	4.2	4.2	54	77.8
Leucocrinum montanum	(3)	0	1	11.1
Lupinus sericeus	5.9	3.3	71	88.9
Microseris nigrescens	.2	0	24	33.3
Myosotis alpestris	.2	.6	55	33.3

(TABLE II. Continued).

Species	Cover		Frequency	Constancy
	C[1]	B[2]		
	%	%	%	%
Oxytropis sericeus	.1	.2	3	11.1
Oxytropis spp.	0	0	4	22.2
Penstemon rydbergii	.3	.2	14	33.3
Perideridia gairdneri	.2	0	8	33.3
Phlox hoodii	1.4	.2	43	55.6
Phlox multiflora	1.0	.1	29	55.6
Polygonum bistortoides	.4	.2	51	88.9
Potentilla diversifolia	.4	.1	20	33.3
Potentilla effusa	0	0	19	33.3
Potentilla gracilis	.9	.9	21	33.3
Potentilla spp.	.1	0	1	11.1
Pulsatilla ludoviciana	.6	.1	33	66.7
Saxifraga rhomboidea	.2	.4	32	55.6
Senecio integerrimus	.1	.1	16	55.6
Silene spp.	0	0	3	11.1
Solidago decumbens	(3)	0	5	33.3
Swertia radiata	.3	0	8	22.2
Taraxacum officinale	.2	.1	13	33.3
Valeriana edulis	(3)	0	1	11.1
Zygadenus gramineus	.5	.5	29	55.6
Total forbs	35.3	25.6		
Rosa spp.	.2	.2	2	11.1
Selaginella densa	1.2	6.8	58	66.7
Total vegetation	100.0	100.0		

[1] Crown.
[2] Basal.
[3] Less than 0.1%.

ing forbs had dried and disappeared. Vernal species seen in or adjacent to the stands but not found in August included sagebrush buttercup (*Ranunculus glaberrimus*), lanceleaf springbeauty (*Claytonia lanceolata*), lomatia (*Lomatium montanum* and *L. orientale*), and violets (*Viola* spp.). A complete species inventory of these stands would require examinations about June 1 and again in August.

Idaho fescue (*Festuca idahoensis*) was present in relatively large amounts in all stands. It clearly dominated the vegetative cover in stands 7, 8, and 9 and contributed significantly to it in the remaining stands (Table II). The other species in the grass-sedge category with high frequency and constancy values were "upland" sedge (*Carex obtusata*) and prairie junegrass (*Koeleria cristata*); however, neither tended to dominate the cover. Other grasses and sedges with high constancy values were: thickspike wheatgrass (*Agropyron dasystachyum*), slender wheatgrass (*Agropyron trachycaulum*), dunhead sedge (*Carex phaeocephala*), and Sandberg bluegrass (*Poa secunda*).

Two species dominated the forbs. Pale agoseris (*Agoseris glauca*) and silky lupine (*Lupinus sericeus*) each provided at least 4% of the vegetative cover, and were in at least 8 of the 9 stands. Avens (*Geum ciliatum*), in 7 stands, also occounted for 4% of the cover. Other forbs were found consistently, indicating they were characteristic components of the cover although not necessarily in great abundance. Species in this category were western yarrow (*Achillea lanulosa*), ballhead sandwort (*Arenaria congesta*), bluebell (*Campanula rotundifolia*), showy cerastium (*Cerastium arvense*), northern bedstraw (*Galium boreale*), and American bistort (*Polygonum bistortoides*).

Crown and basal contacts differed in several ways. Of the 90 species on the plots, crown contact detected 79 (88%) and basal contact detected 61 (68%). There was no real difference between the 2 methods in the proportion of vegetative cover contributed by grasses and sedges—63.3 and 67.4% (Table III). There was a greater difference in the forb category—35.3 and 25.6% by the crown and basal contact, respectively. Further analyses showed these values to be significantly different. The difference may be due to the apparently greater ratio of foliage area to plant base area for forbs than for grasses. Although fewer forbs were detected by the basal contact method, those 37 species that were recorded accounted for 90% of the total forb cover, based on the crown contact procedure. A similar comparison for grasses and sedges showed that those species hit by the basal contact made up 99.7% of the total grass-sedge cover.

Herbage Production

Total air-dry herbage production ranged from 777 to 3,311 lbs/acre, with an average of 1,752 lbs in the 8 stands sampled (Table III). The grasses and sedges averaged 944 lbs/acre, or 54% of the total. Forbs accounted for the remaining 808 lbs. Selaginella was excluded from all herbage production measurements.

There was considerable variation in the grass-forb ratio among stands. Stand 7 was predominantly grass, while stand 2 had the greatest percentage of forbs. In stand 7, Idaho fescue contributed 52% to the total herbage production, and its average contribution for all stands was 19%. Silvery lupine, the only forb individually clipped in every stand, averaged 9% in the total production for all stands. Forbs contributed 50% or more to total herbage production in half the stands. In contrast, the cover analyses showed the grass-sedge group to be the greater contributor in all stands except number 5 (Table II). Similar comparisons showed that silky lupine contributed more to herbage production than to the vegetative cover.

TABLE III. Herbage production (pounds per acre, air dry) for 8 stands, 1955

Species	1		2		3		4		5		6		7		9		Average	
	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%	lbs/A	%
Agropyron spp. (all)	122	7.2	25	1.6	33	3.1	399	12.1	289	12.4	114	5.4	170	15.2	22	2.8	147	8.4
Bromus pumpellianus	22	1.3	—	—	—	—	319	9.6	220	9.5	221	10.4	—	—	—	—	—	—
Carex obtusata	—	—	79	4.9	20	1.9	—	—	—	—	—	—	116	10.3	42	5.4	—	—
Festuca idahoensis	274	16.3	157	9.7	186	17.7	644	19.5	254	10.9	364	17.1	579	51.7	208	26.8	333	19.0
Hesperochloa kingii	552	32.8	144	8.9	94	9.0	—	—	41	1.8	—	—	—	—	9	1.2	—	—
Poa spp. (all)	35	2.1	—	—	—	—	379	11.4	226	9.7	69	3.2	9	.8	45	5.8	—	—
Other grasses & sedges	218	12.9	181	11.2	201	19.1	115	3.5	126	5.4	165	7.8	37	3.3	25	3.2	—	—
Total grasses & sedges	1,223	72.6	586	36.3	534	50.8	1,856	56.1	1,156	49.7	933	43.9	911	81.3	351	45.2	944	53.9
Achillea lanulosa	72	4.3	—	—	—	—	191	5.8	20	0.8	35	1.6	11	1.0	—	—	—	—
Agoseris glauca	—	—	—	—	—	—	—	—	—	—	137	6.5	—	—	—	—	—	—
Antennaria rosea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	4.3	—	—
Aster foliaceus	—	—	—	—	—	—	217	6.6	—	—	—	—	—	—	—	—	—	—
Balsamorhiza incana	—	—	—	—	—	—	—	—	23	1.0	—	—	—	—	—	—	—	—
Chrysopsis villosa	—	—	0	0	58	5.5	—	—	—	—	—	—	—	—	106	13.6	—	—
Galium boreale	(1)	—	22	1.4	37	3.5	—	—	—	—	—	—	—	—	—	—	—	—
Geum ciliatum	(1)	—	—	—	—	—	43	1.3	169	7.3	358	16.8	—	—	—	—	—	—
Lupinus sericeus	147	8.7	240	14.8	(1)	—	339	10.1	377	16.2	135	6.4	9	.8	0	0	156	8.9
Phlox hoodii	—	—	258	16.0	211	20.1	—	—	—	—	—	—	—	—	84	10.8	—	—
Other forbs	242	14.4	510	31.5	211	20.1	665	20.1	583	25.0	527	24.8	189	16.9	203	26.1	—	—
Total forbs	461	27.4	1,030	63.7	517	49.2	1,455	53.9	1,172	50.3	1,192	56.1	209	18.7	426	54.8	808	46.1
Total Production	1,684	100.0	1,616	100.0	1,051	100.0	3,311	100.0	2,328	100.0	2,125	100.0	1,120	100.0	777	100.0	1,752	100.0

[1] Less than one pound per acre.

Protected-Grazed Relationships

Stands 4-9 and their grazed counterparts had similar ground cover component values as determined by basal contacts. Vegetation and litter accounted for 96 and 97% of the ground cover for the protected and grazed stands; bare soil and rock were the other 2 ground cover components. Total vegetation averaged 20.3 and 20.6% for the protected and grazed stands. Although the grazed stands had, on the average, more vegetation, less grasses and sedges, and more forbs than the protected stands none of these differences proved real when analyzed. All comparisons between protected and grazed stands were based on basal contacts to eliminate the effects of current grazing. Unfortunately, stands 1, 2, and 3 had no grazed counterparts.

Species composition of the grass-sedge group often differed markedly between the 6 stands and the adjacent grazed range. These differences and similarities are shown in Table IV. The wheatgrasses (*Agropyron* spp.), pumpelly brome (*Bromus pumpellianus*), Idaho fescue, and inland bluegrass (*Poa interior*) accounted for 64% of the grass vegetation in the protected stands and 32% in the grazed stands. In contrast, there were generally greater percentages of upland sedge, prairie junegrass, Cusick bluegrass (*Poa cusickii*), Sandberg blue-grass, and subalpine needlegrass (*Stipa columbiana*) in the grazed than in the protected stand (58 and 29%, respectively). Other grasses and sedges either showed no definite response or contributed such a small amount to the grass-sedge cover that they could not be adequately evaluated. Idaho fescue made up a greater proportion of the grass cover in the protected stands than in the grazed stands in 5 of 6 comparisons. In stands 7, 8, and 9, Idaho fescue accounted for 54-69% of the grass and sedge cover in contrast to about 28% on the grazed range adjacent to these 3 stands.

Paucity of basal contacts on the forb group tended to mask any clear-cut trends for individual species. However, at all 6 locations there was consistently more pale agoseris and usually more silky lupine in protected than in grazed stands. In contrast, avens, showy cerastium, and western yarrow were more abundant on the grazed than on the protected range.

DISCUSSION

Four species, Idaho fescue, upland sedge, pale agoseris, and silky lupine, are characteristic of the Idaho fescue community in this area. The presence of upland sedge, pale agoseris, and silky lupine with Idaho fescue and the lack of species commonly found with it by Wright & Wright (1948), Daubenmire (1942), and Evanko and Peterson (1955) strongly suggests that a different association is present in the Big Horn Mountains than in the other areas studied. Such differences were found also by Beetle (1956) in

TABLE IV. Grass-sedge composition at 6 grazed and 6 protected stands—basal contact

Species	4		5		6		7		8		9		Average	
	P[1]	G[2]	P	G	P	G	P	G	P	G	P	G	P	G
Agropyron albicans	0	0	1.0	0	3.2	0	0	0	0	0	0	0	0.7	0
Agropyron dasystachyum	6.0	2.4	8.1	3.0	9.3	1.7	3.9	1.3	0	0	2.4	1.7	5.0	1.7
Agropyron subsecundum	0	1.0	1.0	1.0	6.8	3.6	0	0	0	0	0	0	1.3	.9
Agropyron trachycaulum	14.0	1.4	14.2	6.0	2.7	2.5	1.0	0	0	0	0	0	5.3	1.6
Agrostis scabra	0	1.0	1.0	0	0	0	0	0	0	0	0	0	.2	.2
Bromus pumpellianus	20.0	0	9.1	0	4.9	1.4	0	0	0	0	0	0	5.7	.2
Carex obtusata	6.0	21.4	12.2	34.4	20.3	40.3	24.5	40.1	11.9	39.7	12.4	18.7	14.5	32.4
Carex petasata	0	1.2	0	0	0	.6	0	0	0	0	0	0	0	.3
Carex phaeocephala	2.0	0	0	0	0	.8	0	0	0	0	0	0	.3	.1
Danthonia intermedia	0	1.0	1.0	0	.7	.8	0	0	0	0	0	0	.3	.3
Festuca idahoensis	24.0	34.6	18.2	16.3	31.8	28.5	60.8	29.3	68.6	28.6	53.7	25.6	42.8	27.2
Hesperochloa kingii	0	0	1.0	0	0	0	2.0	0	0	0	0	0	.5	0
Koeleria cristata	12.0	17.2	5.1	5.0	.9	0	3.9	6.7	3.0	7.9	8.8	17.8	5.6	9.1
Muhlenbergia richardsonii	0	0	1.0	0	13.8	14.1	0	0	0	0	0	0	2.5	2.4
Poa ampla/canbyi	8.0	15.5	8.0	20.2	1.6	1.1	0	0	0	0	0	0	2.9	6.1
Poa cusickii	0	0	0	0	0	0	1.0	1.3	3.0	4.8	4.9	7.0	1.5	2.2
Poa interior	4.0	0	14.0	1.0	.9	0	0	0	0	0	0	0	3.2	.2
Poa pratensis	4.0	0	0	0	.9	1.6	0	0	0	0	0	0	.8	.3
Poa secunda	0	0	1.0	7.1	2.2	1.6	2.9	21.3	13.5	19.0	17.8	29.2	6.2	13.0
Stipa columbiana	0	3.3	4.1	6.0	0	1.4	0	0	0	0	0	0	.7	1.8
Total grasses & sedges	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[1] Protected.
[2] Grazed.

his more extensive survey of the Big Horn Mountains.

Idaho fescue, upland sedge, pale agoseris, and silky lupine each contributed, on the average, at least 4 and as much as 25% to the vegetative cover. In addition, each had a constancy value of 89% or greater and frequency values of 97, 97, 74, and 71% (Table II). Upland sedge does not influence the general appearance of the vegetation because of its low stature. This sedge is rhizomatous, but does not form a sod; instead it occurs usually in single 3-leafed shoots rarely more than 3-4 in. high. Although seed stalks are taller, the species is still relatively inconspicuous in these stands until the taller vegetation is pushed aside. Because the sedge is inconspicuous, it is best classed as a characteristic rather than a dominant species. Additional characteristic species (constancy of 78% or greater) were slender wheatgrass, thickspike wheatgrass, dunhead sedge, prairie junegrass, Sandberg bluegrass, western yarrow, ballhead sandwort, bluebell, showy cerastium, northern bedstraw, and American bistort.

Stand Analysis

The tables indicate differences among the 9 stands. Stands 1-3 were at the same location but differed in their topographic position and aspect (Figs. 1 and 2). Stands 4-6 were in the same general geographic location and differed primarily in aspect (Fig. 3); these stands were approximately 12 airline miles from stands 1, 2, and 3. The remaining 3 stands were 5-11 airline miles apart and as much as 70 airline miles from stands 1-6. Also, the residual soils in stands 1-6 were derived from sedimentary rocks, while those soils in the remaining 3 stands were from granitic or mixed grantic-sedimentary rocks (Table I, Fig. 4). Vegetation differed among the stands (Tables II and IV, but several species were important contributors to the cover in all stands.

Similarity between and among stands was determined by comparing each stand with every other stand. Cover comparisons based on the

FIG. 1. Stand 1, northeast aspect, deep soils; aspen reproduction in clump at right closely browsed by elk and/or deer.

FIG. 2. Stand 2, a gentle ridge with northwest aspect, shallow soils with limestone rocks on surface.

FIG. 3. Stand 4, north aspect, deep soil from shale and sandstone.

FIG. 4. Stand 8, gentle west aspect, soil from granitic-sedimentary drift, medium depth and droughty.

TABLE V. Similarity indices (in percentage) based on cover estimates in Table II determined by crown contact

Stand	1	2	3	4	5	6	7	8	9
1		59.1	59.1	40.6	46.8	43.5	27.8	28.6	23.7
2			74.7	33.8	36.1	40.3	34.2	41.4	39.3
3				35.6	36.2	38.0	34.2	40.5	39.9
4					66.7	64.7	27.8	31.7	23.3
5						58.3	26.7	29.9	21.8
6							38.7	41.4	33.3
7								67.4	44.6
8									57.9

crown contact procedure were made and the results are in Table V. For every 2 stands compared, the amount of similar cover was added; the total then became the index of similarity. Thus, in comparing stands 1 and 2, *Agropyron subsecundum* provided 0.5% of cover common to both, *Agropyron trachycaulum*, 1.8%; *Agrostis scabra*, 0.9%, etc. (Table II). When totaled, the sum was 59.1 (Table V)—the index of similarity. This procedure was adapted from Hanson (1955).

The 9 stands break into 3 similar groups. Stands 1, 2, and 3 were alike and had an average index of similarity of 64.3. These stands averaged about 63% grasses and sedges and the cover contained substantial amounts of Idaho fescue, spike fescue (*Hesperochloa kingii*), upland sedge, and silky lupine. Stands 4, 5, and 6 were alike and had an average index of similarity of 63.2. In these stands the cover was about equally divided between the grass-sedge and the forb groups. Important species were slender wheatgrass, thickspike wheatgrass, pumpelly brome, Idaho fescue, pale agoseris, avens, and silky lupine. The average index for the remaining 3 stands was 56.6. Here, the grass-sedge group clearly dominated and averaged 76% of the total cover. Idaho fescue was the major species in all 3 stands and upland sedge was common. Sandberg bluegrass contributed more to the cover than it did in the other 2 groups of stands. Although no single forb was a major component of the total cover, silky lupine was the most conspicuous. Selaginella was most conspicuous in these 3 stands.

Indices of 65% or more indicate a high degree of similarity (Hanson 1955). Of the 36 indices of similarity for the 9 stands only 3 were above 65. At the other extreme were 8 values below an index of 30%, with one as low as 22%. Stands 5 and 9 with a 22% index of similarity had little in common except that in both stands Idaho fescue contributed more to the cover than did any other species. Stands 1, 2, and 3 were more similar to stands 4, 5, and 6 than to stands 7, 8, and 9.

Species—Soils—Parent Rock

Although Idaho fescue was prominent in the cover in stands 1-6 having soils derived from sedimentary rocks, it was of even greater prominence in stands 7, 8, and 9 on soils from granitic rocks. In the last 3 stands, Idaho fescue accounted for an average of 46.8% of the vegetative cover (crown contact), and in stands 7 and 9, 41.5% of the total herbage production. In stand 7, judged to be the most productive site of the 3 on soils from granitic rocks and the one protected from livestock grazing for the longest period, Idaho fescue contributed 66.6% to the cover and 51.7% to the herbage production. Stands 1, 4, and 5 were believed to represent the potential for their respective sites. Here, Idaho fescue accounted for 12.7, 12.8, and 12.8% of the vegetative cover (Table II) and 16.3, 19.5, and 10.9% of the herbage production (Table III).

Other species also responded differently to soil and parent rock characteristics. Some species in stands 1-6 were absent or occurred sparingly in stands 7, 8, and 9. They were: bearded wheatgrass (*Agropyron subsecundum*), slender wheatgrass, big bluegrass (*Poa ampla*) and inland bluegrass. Although timber oatgrass (*Danthonia intermedia*) did not occur in stands 7, 8, and 9, it has been reported on granitic soils in more extensive surveys on grazed ranges in this area (Hurd and Kissinger 1952).

Forbs were more abundant in stands 1-6 than in stands 7, 8, and 9. They provided an average of 42.7% of the vegetal cover (crown contact) in stands 1-6 compared with 20.4% for stands 7, 8, and 9. The same relationship was seen in herbage production where forbs produced 48.4% of the total vegetation in stands 1-6 contrasted with 36.8% in stands 7 and 9, although there was great variation between these 2 stands. Soil depths, soil textures, and apparent greater moisture-holding capacity of the soils from sedimentary rocks (Table I) appeared to favor the production of forbs.

Differences apparent among the stands suggested this grass-forb community may have had several facets that were markedly influenced by geology and the derived soils. Generally, soils from granitic rocks were shallower, lighter textured, contained more gravel, and consequently would normally have had lower moisture-holding capacity than soils from limestones, sandstones, and shales in the same general area. Studies are needed on stands occupying essentially the same topographic and geographic positions but differing only in parent material before the effect of parent material can be adequately evaluated.

Species Response to Grazing

In 5 of 6 comparisons Idaho fescue provided a greater percentage of the grass cover in protected than in grazed stands (Table IV). This was particularly evident on the granitic soils (stands 7, 8, and 9) where it averaged 61% of the grass cover on the protected stands compared with 28% on grazed stands. In stand 4 there was more Idaho fescue on grazed than protected range—34.6 and 24.0%, respectively. At this site and perhaps similar sites having deep soil, north exposure, and high moisture holding capacity, other species may be better adapted than the fescue. As seen in Table IV, pumpelly brome assumed an important position in stand 4. On such sites Idaho fescue may be an "increaser" (Dyksterhuis 1949) but additional evidence is needed before it is placed in that group.

Several other species contributed more to the vegetative cover of the protected than of the grazed stands; the reverse was true for still others. Thickspike wheatgrass, slender wheatgrass, pumpelly brome, and inland bluegrass were consistently more abundant in the vegetative cover of the protected range. In contrast, upland sedge, Sandberg bluegrass, prairie junegrass, and subalpine needlegrass provided a greater percentage of the vegetative cover on the grazed range. The big bluegrass-Canby bluegrass (*Poa canbyi*) combination (combined because there were no strong differentiating vegetative characters) and Cusick bluegrass also tended to contribute more to the vegetative cover of the grazed range.

Although response by forbs was not always clear-cut, there were several examples indicating possible trends in reaction to the grazing and protection treatments. Pale agoseris was consistently much more abundant on the protected than on the grazed range. Common forbs such as silky lupine, showy cerastium, and ballhead sandwort showed no consistent response and were more abundant on the grazed range at 3 of 6 locations. Western yarrow and avens were somewhat more definite in that they generally provided a greater amount of ground cover on the grazed than on the protected range.

Summary

The point quadrat method utilizing both crown and basal contacts was used to inventory 9 grass stands at the middle elevations in the Big Horn Mountains. These stands were selected primarily to get quantitative information on the potential vegetative development and productivity of the site. Consequently, they were either protected from livestock grazing or had been grazed only

lightly for as long as 30 yr. For comparative purposes adjacent areas grazed by cattle were also examined whenever possible.

Idaho fescue is the most important single species from the standpoint of cover, herbage production, frequency, and constancy. As a result, these well-drained upland sites, characteristic of much of the grasslands, are commonly referred to as the "Idaho fescue type." The frequency, cover, and stature of silky lupine and its contribution to the general appearance of the herbaceous vegetation suggests that *Festuca idahoensis-Lupinus sericeus* association would be an appropriate and descriptive name.

Grasses and sedges accounted for about 65% of the vegetative cover, with forbs making up most of the remainder. Forbs were more characteristic of the stands on those soils derived from sedimentary rocks than those stands found on soils from granitic rocks. The opposite was true for selaginella. Although grasses and sedges contributed more to the vegetative cover than forbs, they accounted for only 31% of the 90 species on the sample plots.

Percentage cover of grasses and sedges, forbs, bare soil, and litter was essentially the same for paired comparisons on protected and grazed ranges. Composition of the vegetal cover varied considerably. Idaho fescue, thickspike, slender and bearded wheatgrasses, and pumpelly brome were more abundant on protected ranges than grazed ranges. The opposite was true for upland sedge, prairie junegrass, Sandberg and Cusick bluegrasses, and subalpine needlegrass. The combined big and Canby bluegrasses also tended to be more abundant on grazed range. The response of individual forbs was less clear-cut because of more species and lesser amounts of cover involved. Pale agoseris consistently contributed a greater percentage to the vegetative cover on protected than grazed range.

Point quadrat analyses by the crown contact method detected 79 of the 90 species present. The basal contact method detected 61 species. Both methods gave essentially the same results for the grass-sedge group (63.3 and 67.4%), whereas forbs accounted for 35.3% of the vegetative cover based on crown contact method compared with 25.6% by the basal contact method. Relatively close agreement on important components of the vegetation suggests the basal contact method would be particularly useful to eliminate effects of differential grazing to species or areas on currently grazed ranges. This method would probably be less influenced by current growing conditions and the effect these have on foliage production.

Herbage production in 1955 ranged from 777 to 3,311 air-dry lbs/acre, with those stands on soils from sedimentary rocks producing the greatest amount per acre. Grasses and sedges accounted for about 54% of the total vegetation; forbs comprised the remainder. Forbs contributed, on the average, about 46% to herbage production compared with 26 and 35% to the vegetative cover by the basal contact and crown contact methods, respectively. Idaho fescue in 8 stands produced an average of 333 lbs/acre, or 19% of the total production, although greatest production was 644 lbs/acre. This amount was again 19% of the total for the stand. In another stand it provided 52% of the total production.

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PHYTOSOCIOLOGICAL STUDY OF BURNED DECIDUOUS WOODS, TURTLE MOUNTAINS NORTH DAKOTA[1]

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INTRODUCTION

One of the most interesting and unique areas in North Dakota for its physiography and vegetation is the Turtle Mountains. This oval-shaped area of glaciated hills is in north-central North Dakota and southern Manitoba, with the International Boundary lying along the east-west longitudinal axis. The area in the U.S. includes northern portions of Bottineau, Rolette, and Towner counties, distances of about 43 miles east-west and 14 miles north-south. The Turtle Mountains are an outlying remnant of the Missouri Plateau now separated from the main escarpment by a Drift Plain which is 30 miles or more wide. The hills, with a general elevation of 2100-2200 ft and a maximum elevation of 2300 ft on Butte St. Paul, are about 600 ft above the surrounding plain. The general topography is hilly with intervening depressions filled with ponds of variable duration and by permanent lakes, many of which are spring-fed.

The general region has cold, dry, long winters and warm summers with about 75% of the annual precipitation during the growing season. Bottineau, at 1635 ft at the southwest edge of the Turtle Mountains, has an annual average precipitation of almost 16 in. There are no meteorological stations in the hills. Although winter temperatures may not be greatly colder, the summer ones are definitely cooler in the hills due to the lakes, forests, and the increased altitude. The combined effect of cooler temperature and increased altitude results in an increase of snow and rain. Crops on small cleared plots rarely suffer from excessive drought which may occur in the surrounding plains.

The Turtle Mountains contain the largest area of the Canadian Zone in North Dakota (Bailey 1926). Spruce, fir, and hemlock of this zone are no longer present; aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) compose a major share of the forest. They are particularly dense on north-facing slopes where deep snows linger late in the spring. Also present are balsam poplar (*Populus balsamifera*), bur oak (*Quercus macrocarpa*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), and boxelder (*Acer negundo*). The forest is interrupted by small grasslands on southern exposures of ridges, by more extensive openings of sedge meadows or marshes on old lake beds, and by presently existing open lakes. Nelson (1948), in a report on forestry in North Dakota, stated that there were 90,000 acres of forest on the U.S. side of the Turtle Mountains; this represents about half of the area. Today, numerous small sawmills are cutting aspen, elm, and oak.

Pollen analysis (Potter, unpubl.) of the shallow peat deposits shows coniferous pollen to nearly the surface. The climatic conditions and the acid peat are ideal for the growth of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) which are common in stands under similar conditions 200 miles east in Minnesota, and in the Spruce Woods Forest Preserve of the Asiniboine River Valley, the southern edge of which is about 60 miles northeast. This stand was surrounded by prairie prior to settlement and cultivation; however, it occurs on a sandy embayment of former Lake Agassiz, part of which represents stabilized sand dunes. The soil and climatic conditions of the Turtle Mountains are amenable to spruce: planted spruce matures successfully and produces seed leading to volunteer seedling establishment.

The only connection to the boreal forest of Northeastern North America is via the stream galleria of streams draining eastward. These galleria are composed entirely of deciduous tree species. The absence of conifers in the Turtle Mountains is probably the result of frequent fires in dry years when water levels were low and conifer stands bordering depressions were dry enough to completely burn out. Water level fluctuations are great and there is ample evidence of fire. Aspens, with their abundant, widely dispersed, airborne seeds quickly populate areas after fire, sprout vigorously and are very competitive resulting in their usual post-fire dominance.

In 1886 a prairie fire starting south of the Turtle Mountains near Dunseith burned into the forested hills and continued until it had consumed the forests of essentially all of the Turtle Mountains. Because of the numerous lakes, some extensive and sprawling, some isolated areas probably escaped complete burning. However, a

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long-time study of periods of drought by tree ring analyses of bur oak in the central part of the state by Will (1946) indicates a 14 yr drought from 1877-1891. This was the longest drought period from 1836-1922 and the lake levels were undoubtedly lowered; fire at this time could have resulted in maximum damage. That several islands in Lake Metigoshe were unburned, or only slightly burned, is evidenced by large bur oak and American elm exceeding in age the interval of time since the fire. For example, in 1948 a 34.9 in. dbh elm was determined to be 280 yr old and a 36.6 in. dbh bur oak to be 570 yr old. These were among the largest trees on Masonic Island (Nelson 1948).

Interest in fire as a major factor affecting the vegetational history of the Turtle Mountains was the principal instigation for this study. It was desired to make a comparison of unburned or lightly burned, sites with sites which had been severely burned and which had similar soil type, exposure, and drainage. Comparisons are based on phytosociological data derived from a modification of the arms-length rectangle method of Penfound and Rice (1957). Frequency, density, basal area, and importance percentage of trees are given by size classes of one in. dbh increments. The distribution among the size classes is indicative of the history and future trends of each species. Comparisons are also made of shrub and herbaceous vegetation. To determine the effect of burning and nature of recovery of soils and surface organic matter, detailed comparisons of soil profiles of several sites are presented. The nomenclature for plant species follows that of Stevens (1950).

With the assistance of a grant-in-aid from the North Dakota Institute for Regional Studies at North Dakota State University, a study was made of the vegetation and soils of several stands in the summer of 1958. Acknowledgement is made to Mr. Duane Green, Assistant State Forester, for general assistance; to Mr. Hollis Omodt, North Dakota Soil Survey and Mr. Armand Bauer, North Dakota Soil Testing Laboratory, for field assistance; and to Dr. Enoch Norum and the Department of Agronomy (Soils) of the North Dakota Agricultural Experiment Station for laboratory analyses of soils.

Methods

Selection of Sites

The rare isolated unburned areas were located by interview with long-time residents and personnel of the State Forestry office at Bottineau, followed by detailed examination of stereo pairs of aerial photos.

The most extensive stand of large trees apparently uncut and unburned was an area locally called "Scully's Woods." This stand is northwest of Lake Francis in the S.E. ¼ of Sec. 32, T164N, R75W in Bottineau County. The area was examined from stereo pairs and the stand of large timber outlined. By ground reconnaissance aerial photos were checked and boundaries arbitrarily determined. Adjacent and to the west of this stand and within the same quarter section is an area of similar topography which was obviously burned. The evidence of burning consists of charcoal fragments, the lack of large mature bur oak predating the fire of 1886, and the prevalence of dense stands of aspen of an age post-dating the fire. This stand is referred to as "Scully's Woods—Burned" and the control as "Scully's Woods—Unburned." The use of "unburned" is not meant to be absolute for there may have been some ground or brush fire, but such fire did not destroy the main stand of timber.

A third stand studied is between Boundary Lake and Hartley Lake in the N.W. ¼ Sec. 36, T164N, R74W and in the S.W. ¼ Sec. 25, T164N, R74W of Bottineau County. Here the terrain is level, the soils are of fine texture, and the drainage is poor. An abundance of charcoal just above the mineral soil and the even-aged stand of mature aspen indicate a past severe fire. There was not an unburned stand on a similar site or soil for comparison.

Methods of Sampling Vegetation

The sampling technique selected was determined by the purpose of the study, the size and nature of the stands, and the time and manpower available. Because of the density of brush and understory trees, laying out quadrats was too time consuming. To include a greater number of the variations of the undulating topography, a method using many plots distributed over a wide area or along many transect lines seemed desirable. The most satisfactory method was a modification of the arms-length rectangle method of Penfound and Rice (1957).

By this method a worker determines the span of his out-stretched arms and then samples a rectangle of appropriate length to equal an area of 0.01 acre. If, for example, the width was equal to 6 ft, a distance of 72.6 ft would be sampled in each plot. In traversing each sample plot, the species and dbh of each tree are announced to and recorded by a companion. Because of the difficulty of pacing off the distance accurately in dense

hazelbrush and over irregular topography, the distance of each rectangle was determined not by pacing but by the length of a heavy cord which was tied to the belt of the first worker and dragged behind. The recorder, standing at the beginning point of the rectangle, aided in keeping the first man in proper compass alignment and stopped him when the end of the cord reached the starting point. The recorder then moved forward and the process was repeated. In each stand a total of one acre or 100 rectangular plots of 0.01 acre size was sampled. In the unburned stand this represented about a 10% sample, well above the recommended rate of Penfound and Rice (1957) and was on a type which had a tree density 3-6 times greater.

From the data, measures of frequency index, relative frequency, density per acre, relative density, square foot basal area per acre, relative basal area, and importance percentage for each species were calculated. The last was the sum of relative frequency, relative density, and relative basal area (Curtis 1947, Curtis and McIntosh 1951) divided by 3. In addition, information was obtained to derive the distribution of number and percentage of each species among the size classes, the percentage of each size class made up of each species, the basal area of each size class by species, and the total basal area of all species for each size class. Size classes are based on dbh measurements.

To measure frequency and foliage cover of shrubs and trees less than one in. dbh but more than 4 in. tall a 1/250 acre circular plot (7.45 ft radius) was examined at every fifth rectangular plot. Total foliage cover of the stratum was recorded as well as the percentage of the total cover made up by each species to the nearest 5%. Thus, 8% of an acre area was sampled in each stand.

At every fifth rectangular plot the cover of herbs and seedlings less than 4 in. tall was examined in a 0.5×1M quadrat. The total foliage cover and the percentage of the total to the nearest 5% which was comprised by each species were recorded.

From the data obtained for the shrub and herb strata, expressions were derived for frequency index, relative frequency, total foliage cover, and relative cover. There is no figure comparable to the importance percentage for the tree stratum because no density data were available for the shrubs and herbs.

Sampling of Soil

A comparison of the soil development of the 3 timber stands was attempted. Because of the undulating topography, wide variations occur in soil profiles from locally moist sites to drier sites on the crest of knolls. Water penetration, surface water run-off, soil erosion and deposition, root growth, and plant density all vary with degree of slope and slope exposure. To avoid the local variations and to make the fairest comparison of the effects of fire and differences in forest vegetation on soil development, soil pits were studied in detail on the crest of knolls and on southerly exposed slopes just below the crests. These sites most nearly represent the regional soil development.

Two soil pits were dug and analyzed in each of the stands in Scully's Woods. One represented the well-drained site on the crest of a knoll; the other was midway down the southeast or southwest slope of the knoll. One representative pit was examined from the Boundary Lake stand, which was uniform in relief and vegetation. Each soil was classified to the soil series to which it belonged. Measurements and notes were made of the depth, texture, structure, and color of the horizons in each profile and samples of the mineral soil were obtained, not at fixed depths, but from within each horizon. Each sample of a quart in volume was composited from many small fractions from around the sides of the pit. These samples were air-dried, and analyzed for pH, soluble salt content from electrical conductivity, organic carbon, exchange capacity, moisture retention, and texture according to procedures outlined in United States Department of Agriculture Handbook No. 60 (1954).

Results and Discussion

Tree Stratum

Scully's Woods, Unburned.—The unburned control area had the general appearance of a mature deciduous forest with a favorable distribution of reproductive stock along with the mature size classes of the dominant species. A typical view (Fig. 1) contrasts with the dense stand of aspen on the adjacent burned area (Fig. 2). In the former stand, mature bur oaks were 19-24 in. dbh with straight, tall trunks having little branching in the lower portions, which indicated previous growth under forest conditions. American elms reached 24 in. dbh.

In Figure 3 are density curves for the 4 major species in the unburned stand. These represent the relative number of trees of each species occurring in each of the several dbh classes. The curve for bur oak indicates the most uniform distribution in all size classes with a peak of representation in the 3 in. dbh class. There is a

FIG. 1. The unburned Scully's Woods stand showing the large, straight-boled oaks which reach trunk diameters of 26 in. and pre-date the 1886 fire.

FIG. 2. The dense aspen stand on the burned-over area of Scully's Woods.

relatively high representation in the dbh classes over 12 in. in diameter, indicating the maturity of bur oak and its position as the principal dominant. Its success as a continuing dominant is indicated by the abundance of reproductive stock. The dominance of bur oak in the mature class is more obvious in regard to basal area. Figure 4 indicates the distribution of relative basal area of trees of each species occurring in each of the several dbh classes. The curve for bur oak shows a general percentage increase with increasing size class.

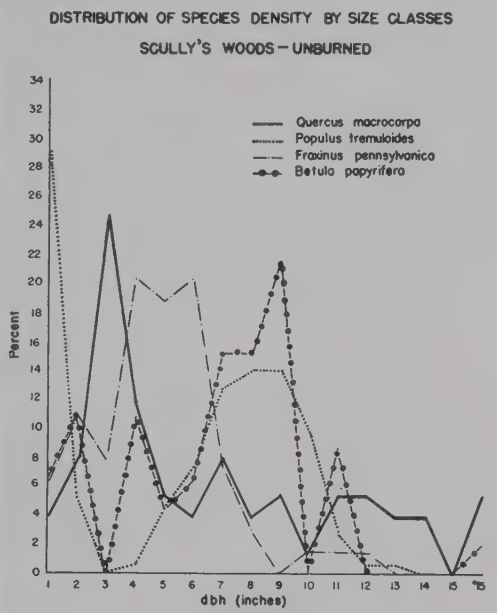

FIG. 3. The distribution of species density by size classes in Scully's Woods, Unburned for the 4 major species.

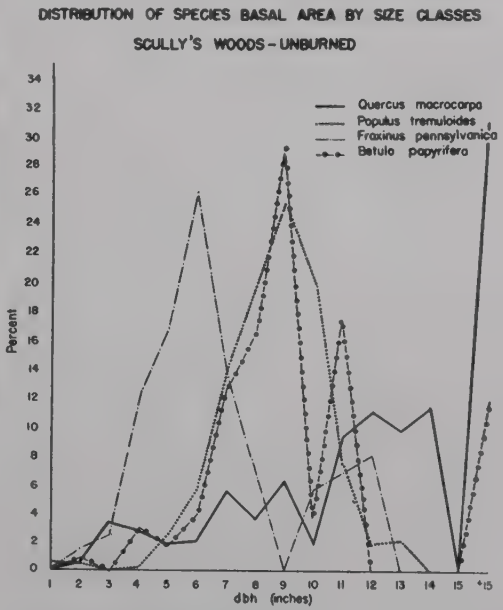

FIG. 4. The distribution of species basal area by size classes in Scully's Woods, Unburned for the 4 major species.

These trees easily predated the 1886 fire. No growth rate curves are available from this area for bur oak, but Nelson (1948) includes figures of 43 yr for 5 in. dbh oak and 570 yr for 36.6 in. dbh oak from Masonic Island. A section of bur oak cut from the Scully's Woods was 15 in. dbh and 193 yr old. Some of the largest oaks in the study area were 19, 23, 24, and 26 in. dbh.

An evaluation of the importance of each of the 4 major species by size classes is in Figure 5. This shows the importance percentage figures, which were derived within each size class. Bur oak was most important in the larger size classes and in the 3 in. class.

The distribution of numbers of aspen by size classes (Fig. 3) followed a normal curve between the 3 and 14 in. diameter classes. Aspens in this area are 60-70 yr old when 8-9 in. dbh. Even a 19 in. aspen taken from these woods in 1948 was dated by the North Dakota School of Forestry personnel as 61 yr old, indicating an initial growth in 1887. The importance of these size classes was related to the fire of 1886 with development either as seedlings or as sprouts. The initiation of aspen growth just after the fire suggests that either aspen is a normal component of the deciduous forest on these sites, or that the area was actually burned over, even though lightly. A ground fire removing some of the ground herbs and brush would have opened up the area sufficiently for the invasion of aspen from surrounding areas or for an increase from existing aspen trees. The total number per acre of aspen trees above the sapling size (4 in. dbh) is 118 in this stand in contrast to 324 per acre in the adjacent burned-over stand.

The lack of aspen in the 3 in. dbh class is interesting. Aspens 2½-3 in. dbh require about 20-24 yr for growth in this area. This means that the 3in. class trees should have started growth in the mid-thirties. One of the most severe droughts of recent time occurred in the Northern Great Plains in 1934-36. Water levels were greatly depressed and drought effects were felt even under the more favorable moisture conditions of the hills. Seedling reproduction and sprout development of aspens would have been at a minimum during these years. Under the more favorable moisture conditions of the 1940's, aspen reproduction was extensive, as indicated by the large percentages in the one and 2 in. classes.

The basal area curves of Figure 4 show a normal distribution of aspen with a definite peak in the 9 in. class. The importance curves of Figure 5 show the combined effect of frequency,

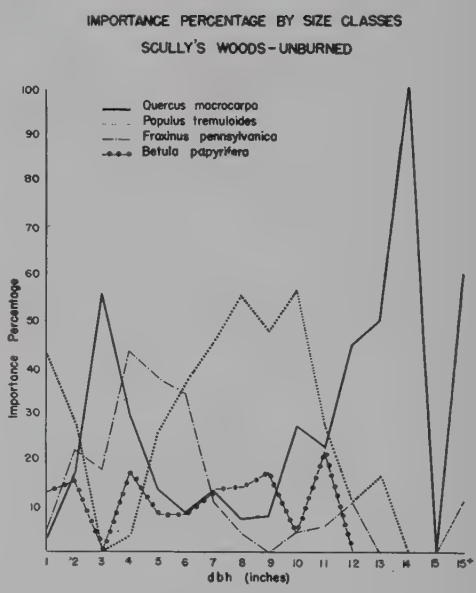

Fig. 5. The importance percentages by size classes in Scully's Woods, Unburned for the 4 major species.

density, and basal area with maxima in the one in. and 8-10 in. classes.

Green ash reached its maximum density, basal area, and percentage importance in the 4-6 in. size classes (Figs. 3, 4, 5). From 37-43% of all the trees in the 4, 5, and 6 in. classes were green ash. A secondary increase in importance of green ash occurs in the 10-12 in. classes. Green ash trees were slender, representing a species successfully reproducing and developing under forest conditions.

The curves of Figures 3-5 show that the size class distribution of paper birch was similar to that of aspen in regard to density and basal area. The frequency indices of size classes of birch are lower than for aspen and the total number of birch per acre amounted to about one-fourth that of aspen. Thus, there is a difference in the form of the curves of the two species for the importance percentage. However, the relative importance of paper birch and its presence in the reproductive classes particularly on slopes toward lake shores was reminiscent of the Lake States coniferous and northern hardwood stands.

A study of the importance percentages (Fig. 5) of size clases from small to large indicates a shift in importance from aspen to oak, ash, aspen, and finally to oak again.

The density per acre and the percentage of trees of the 4 major species are as follows: bur

TABLE I. Analysis of trees > one inch dbh (100 0.01 Acre Plots)

	Scully's Woods-Unburned				Scully's Woods-Burned				Boundary Lake-Burned			
	Rel. Freq.	Rel. Den.	Rel. Basal Area	Imp. %*	Rel. Freq.	Rel. Den.	Rel. Basal Area	Imp. %*	Rel. Freq.	Rel. Den.	Rel. Basal Area	Imp. %*
Populus tremulodies	25.6	37.8	37.0	33.5	50.0	69.8	85.4	68.4	43.3	66.6	86.9	65.3
Quercus macrocarpa	16.0	16.0	24.1	18.7	7.7	3.4	2.5	4.5	3.5	1.4	2.0	2.3
Fraxinus pennsylvanica	16.4	13.5	8.2	12.7	17.0	9.8	2.6	9.8	12.3	5.1	3.5	7.0
Betula papyrifera	8.7	10.1	10.8	9.9	8.8	6.5	6.6	7.3	0.9	0.1	<0.1	0.3
Ulmus americana	8.2	5.7	10.2	8.0	2.8	1.1	1.3	1.7	—	—	—	—
Populus balsamifera	6.9	4.4	6.1	5.8	4.4	2.8	1.5	2.9	14.1	6.8	4.9	8.6
Amelanchier alnifolia	8.7	5.7	0.1	4.8	3.9	3.2	0.1	2.4	9.3	5.1	0.4	4.9
Acer negundo	5.5	3.6	3.4	4.2	2.8	1.1	0.1	1.3	0.9	0.2	0.1	0.4
Prunus virginiana	3.2	3.2	0.1	2.2	2.8	1.5	0.1	1.5	3.1	1.2	0.1	1.5
Salix missouriensis	0.5	0.2	0.01	0.2	—	—	—	—	12.8	13.4	2.1	8.8
Viburnum trilobum	0.5	0.2	0.01	0.2	—	—	—	—	0.4	0.1	<0.1	0.2
Craetegus rotundifolia	—	—	—	—	—	—	—	—	0.4	0.1	0.1	0.2
Total density/acre	—	476	—	—	—	465	—	—	—	950	—	—
Total basal area/acre (sq ft)	—	—	120	—	—	—	113	—	—	—	97	—

* Imp. %=Importance Percentage which is the average of relative frequency, relative density, and relative basal area.

oak 76 (16.0%), aspen 179 (37.8%), green ash 64 (13.5%), paper birch 48 (10.1%), and all other species 109 (22.6%). The basal area in square feet per acre and the percentage were as follows: bur oak 28.5 (23.7%), aspen 43.8 (36.4%), green ash 9.8 (8.1%), paper birch 15.1 (12.6%), and all others 11.5 (19.2%). The total number of trees per acre of all species was 476 with a basal area of 120 sq ft.

A summary of the relative frequency, relative density, relative basal area, and the importance percentage for all size classes of each species is in Table I. The 4 species discussed above comprise 77% of the total density and 80% of the basal area.

Two other species in the large tree class are American elm and balsam poplar. Elm numbers one to 4 trees per acre in nearly all sizes except the one and 2 in. classes. Balsam poplar is represented in the one to 2 in. classes and in the 7-10 in. classes with some trees up to 16 and 18 in. dbh.

The understory trees, in decreasing order of importance, are Juneberry (*Amelanchier alnifolia*), boxelder, chokecherry (*Prunus virginiana*), Missouri willow (*Salix missouriensis*), and highbrush cranberry (*Viburnum trilobum*).

Scully's Woods, Burned.—The list of tree species for the area differs from that of the unburned site in the absence of Missouri willow and highbrush cranberry, resulting in a coefficient of community of 82%. The order of importance of the tree species is changed principally by a reduction of bur oak from 2nd to 4th in importance and of American elm from 5th to 7th. Aspen exceeded oak in importance by less than twice in the unburned stand; here it exceeds oak by more than 15 times. A general view of this stand is in Figure 2.

The number of bur oak trees in the burned stand is about ⅕ that of the unburned stand with a few scattered trees in the several size classes but only one tree over 8 in. dbh. The highest percentage of bur oak trees is in the 4 in. size

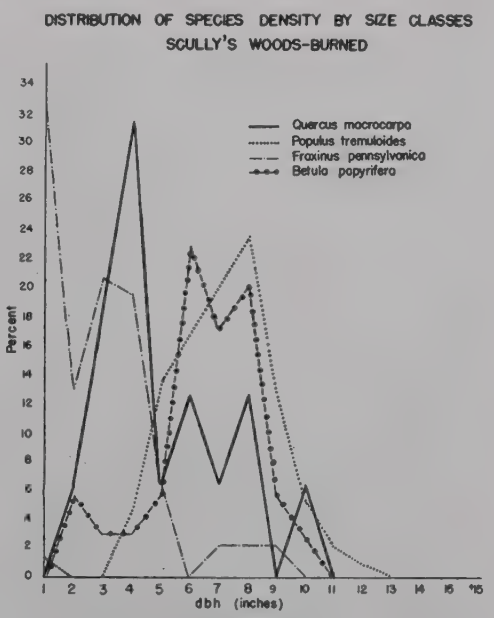

FIG. 6. The distribution of species density by size classes in Scully's Woods, Burned for the 4 major species.

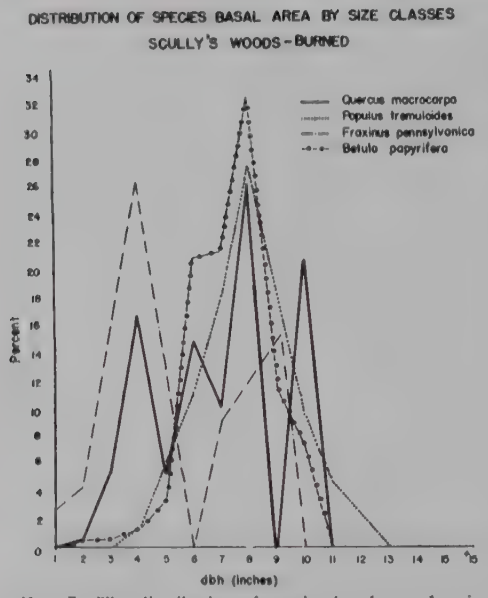

FIG. 7. The distribution of species basal area by size classes in Scully's Woods, Burned for the 4 major species.

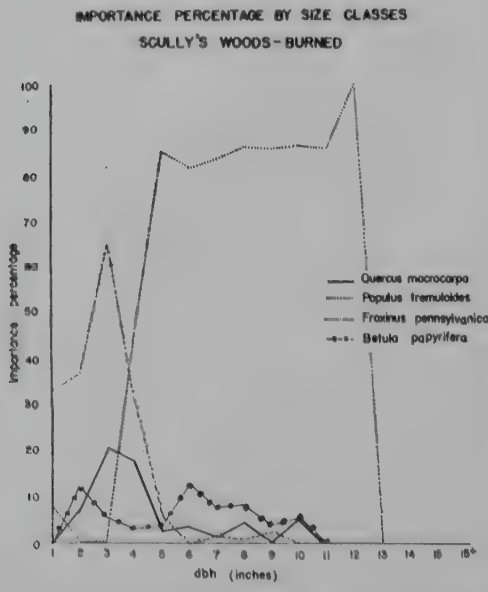

FIG. 8. The importance percentages by size classes in Scully's Woods, Burned for the 4 major species.

class (Fig. 6) indicating the possibility of oak recovery under the aspen canopy. Figure 7 illustrates the lack of basal area in the mtaure class of bur oak which contrasts with the unburned stand. The minor importance of bur oak in the burned stand is best illustrated by the curve for importance percentage (Fig. 8).

Density of aspen again shows a normal distribution curve among the several size classes (Fig. 6). An unusual distinction from the unburned stand is the relative absence of any young reproductive stock in the one, 2, and 3 in. classes. The reason for the absence of young reproductive stock here but its prevalence in the unburned stand is not known. The majority of aspens are in the 8 in. size class. The distribution of basal area among the size classes is similar to the unburned stand; the influence of reduced small stock is slight in its effect on basal area (Figs. 7 & 4). The significance of aspen becomes most obvious on examination of the importance percentage curves of Figure 8. Aspen exceeds the other species in all except the one to 3 in. size classes.

Green ash is most important in the reproductive size classes in comparison with the number of all species, with the relative density distribution within the one species (Fig. 6), and with the relative importance percentage (Fig. 8). Maxima of basal area, however, occur in the 4 and 9 in. class (Fig. 7).

Paper birch is of minor significance with maxima of density in the 6-8 in. classes, of basal area in the 8 in. class, and with importance percentages which are uniformly low. As with aspen, birch may develop rapidly from sprouts following a fire.

In the burned woods, there is a shift in dominance indicated by importance percentage from green ash in the reproductive sizes to aspen in the larger size classes (Fig. 8). The density per acre and the percentage of trees of the 4 major species are as follows: bur oak 16 (3.4%), aspen 328 (69.8%), green ash 46 (9.8%), paper birch 30 (6.5%), and all other species 45 (10.5%). The total number of trees per acre is 465 with a basal area of 113 sq ft, which is nearly identical to that of the unburned stand. The basal area in square feet per acre and the percentages are as follows: bur oak 2.7 (2.3%), aspen 96.9 (85.5%), green ash 3.0 (2.6%), paper birch 7.5 (6.6%), and all others 3.3 (3.0%).

A summary of the relative factors and the importance percentage for all species is in Table I. The 4 species discussed above make up 89.5% of the total density and 97% of the basal area. The importance percentage of aspen is double and that of bur oak is less than one-fourth that of the unburned stand.

Boundary Lake, Burned.—This stand is not

comparable to the other 2 in soil character or drainage. It is typical of many areas of more level terrain and heavy silt or clay soils and was heavily burned over. The total list of species differs from that of Scully's Woods by the absence of American elm and the addition of hawthorn (*Crataegus rotundifolia*), represented in the 100 quadrats by only one tree. The coefficient of community in comparison to the unburned stand is 91%. On the more level, wetter, and finer soils of this site the species importance is considerably changed.

The 4 species of greatest importance are aspen, Missouri willow, balsam poplar, and green ash in descending order of importance (Table I). In the poorly drained, wet soil conditions of this stand, bur oak, which requires improved drainage and aeration, probably never was a dominant tree.

The relative density of aspen in the various size classes varies from 54% to 100%. The basal area of aspen exceeds all other species and represents more than half the total basal area in every size class. The real dominance of aspen is illustrated by the importance percentages (Fig. 9). A few large aspens, up to 14 in. dbh, represent the first generation of regrowth probably from sprouts in areas where the soil was not burned very deeply.

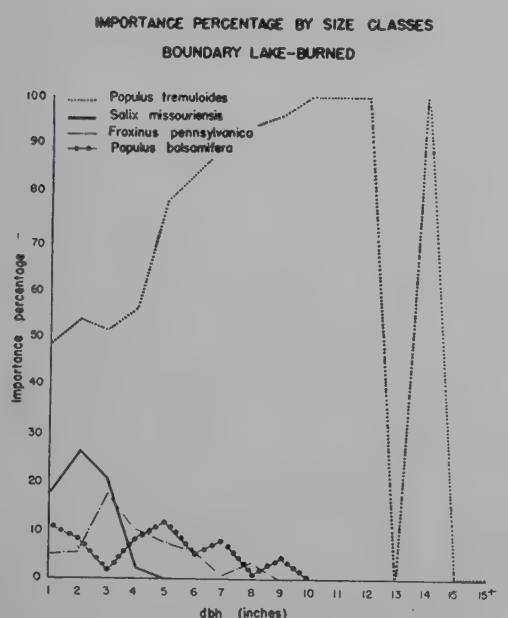

FIG. 9. The importance percentages by size classes in the Boundary Lake, Burned stand for the 4 major species.

Missouri, or diamond, willow is of 2nd importance principally because of its large number of individual stems. In low, heavy soils of poor drainage it responds favorably by producing dense clumps with individual stems up to 4 in. in diameter. In determining density it was necessary to count each stem over one inch in diameter. The importance of this species in basal area was very slight.

Balsam poplar was principally important in the one inch reproductive class, but was represented in the regrowth by trees up to 9 in. dbh.

Green ash was 4th in importance due to its low relative density.

The density per acre and relative density for the 4 major species were as follows: aspen 633 (66.6%), Missouri willow 127 (13.4%), balsam poplar 65 (6.8%), green ash 48 (5.1%), and all others 83 (8.1%). The basal area in square feet per acre and percentages were as follows: aspen 84.2 (86.9%), Missouri willow 2.1 (2.1%), balsam poplar 4.8 (5.0%), green ash 3.4 (3.5%), and all others 2.4 (2.5%).

The relative factors and the importance percentages are summarized in Table I for all species. Due to the high number of small trees and the lack of large mature ones, the total number of trees per acre was 950, or double that of the other 2 stands, but the total basal area of 97 sq ft per acre was considerably less.

Shrub Stratum

No actual count was obtained for the shrub stratum so the importance of the species within this stratum was evaluated only in terms of frequency and coverage. Table II summarizes the shrubs and trees less than one inch dbh and more than 4 in. high for the 3 sites. The species arrangement is in decreasing order of relative cover for Scully's Woods, Unburned. The ranking of the top 10 species is given for the other 2 stands.

The average shrub foliage cover for the unburned site was 45%, for the adjacent burned site 48%, and for the Boundary Lake site 35%. The total species amounted to 20 in the unburned stand. Of these all but *Salix missouriensis* were in the adjacent burned stand. In addition *Cornus canadensis, Lonicera dioica,* and *Viburnum edule* brought the total species to 22 and gave a coefficient of community of 86% in comparison to the unburned stand. *Lonicera villosa, Viburnum lentago, Ulmus americana* and *Betula papyrifera* of the unburned area were not present in the Boundary Lake stand. The latter 2 species were also absent in the tree stratum. Additional spe-

TABLE II. Analysis of shrubs and trees over one inch dbh and less than 4 in high (20 1/250 acre plots)

Species	Scully's Woods-Unburned*			Scully's Woods-Burned			Boundary Lake-Burned		
	Rank	Rel. Cover	Rel. Freq.	Rank	Rel. Cover	Rel. Freq.	Rank	Rel. Cover	Rel. Freq.
Corylus cornuta	1	55.5	11.1	1	79.8	10.3	1	48.5	10.9
Prunus virginiana	2	8.7	9.3	3	4.1	9.7	2	20.1	10.3
Amelanchier alnifolia	3	7.2	5.6	2	4.9	6.2	3	11.0	8.0
Symphoricarpos occidentalis	4	6.8	10.5	8	1.2	9.7	6	4.2	11.5
Fraxinus pennsylvanica	5	5.8	6.2	4	3.9	6.7	4	9.2	8.0
Viburnum trilobum	6	4.1	6.2	5	1.7	6.2		0.5	2.9
Populus balsamifera	7	3.8	1.9		0.1	0.5		<0.1	0.6
Ribes sp.	8	3.7	6.2	9	1.2	5.6		0.3	3.4
Cornus stolonifera	9	1.3	1.9		0.1	1.0	5	4.6	5.2
Populus tremuloides	10	1.2	6.2		0.8	5.6	9	1.0	3.4
Rubus idaeus		1.0	6.8		0.5	4.6	8	1.1	6.9
Total Herbage Cover, %		45.0			48.0			35.0	
Total Number of Species		20.0			22.0			18.0	

* Species with less than 1% relative cover in the unburned stand: *Rubus pubescens, Lonicera villosa, Ulmus americana, Rosa acicularis, Acer negundo, Quercus macrocarpa, Betula papyrifera, Salix missouriensis, Viburnum lentago, Viburnum edule, Lonicera dioica, Cornus canadensis, Viburnum affine.*

cies included *Viburnum edule* and *Viburnum affine,* giving a total of 18 and a coefficient of community of 89% in comparison to the unburned stand.

Corylus cornuta (beaked hazelnut) dominated the shrub layer, averaging over 61% of the shrub cover in the 3 stands. The most obvious influence of fire is the increase in relative cover of *Corylus cornuta* from 55.5% in the unburned stand to 79.8% in the burned stand. This species is apparently less favored by the heavy clay soils of the Boundary Lake burned stand. Of the 3 dominant species of shrubs *Corylus cornuta* was first and *Prunus virginiana* or *Amelanchier alnifolia* second or third in all 3 stands. It is difficult to explain the fact that seedlings of both green ash and bur oak had greater relative cover and relative frequency percentages in the Boundary Lake stand than in the unburned stand. Conversely, the reproductive stratum of the dominants (aspen and balsam poplar) were less important in the burned Boundary Lake stand than in the unburned stand. This apparently attested to the nurse-crop effect of aspen under which other deciduous species such as oak and ash may reproduce and to the control of these latter species once established. Controlling factors may not have prevented seed germination but apparently reduced the successful development of seedlings.

Many of the shrub species are typical representatives of the northern coniferous boreal forest and of the Canadian Life Zone, including *Cornus canadensis, Lonicera villosa, Rubus idaeus, Viburnum edule,* and *Viburnum trilobum.*

The 3 dominant shrubs, *Corylus cornuta, Prunus virginiana,* and *Amelanchier alnifolia* are typical of drier deciduous woods and forest-prairie margins and of the stream galleria which connect the Turtle Mountain area with the deciduous forest region of Minnesota.

The greatest number of species belong to the deciduous forest-prairie border type of shrubs which extend across the plains from the deciduous forests on the east to the Rocky Mountain forests.

There are no representatives of a strictly Rocky Mountain flora in the Turtle Mountains.

Herb and Seedling Stratum

Actual counts of density were not made for this stratum so the importance is based on coverage and frequency. The species are arranged in Table III in decreasing order of relative cover in the unburned stand. Total foliage cover amounted to 60, 41, and 66% in the Scully's Woods Unburned, Burned, and Boundary Lake stands respectively. The total number of species was 40, 39, and 39 in the 3 stands with a coefficient of community of 82% for the Scully's Woods burned stand and 72% for the Boundary Lake stand. The species present in the unburned stand, not elsewhere, were *Anemone canadense, Disporum trachycarpum, Ranunculus abortivus, Mentha arvensis,* and *Viburnum edule.*

The dominant herb in all 3 stands was *Aralia nudicaulis* (wild sarsaparilla). This species, typical of moist deciduous woods, provided 28% of the herbaceous cover in the unburned stand. It was apparently favored by conditions following burning as indicated by an increase to 41% in

TABLE III. Analysis of herbs and seedlings (20 1 × 0.5 Meter Quadrats)

Species	Scully's Woods-Unburned*			Scully's Woods-Burned			Boundary Lake-Burned		
	Rank	Rel. Cover	Rel. Freq.	Rank	Rel. Cover	Rel. Freq.	Rank	Rel. Cover	Rel. Freq.
Aralia nudicaulis	1	28.1	7.9	1	41.5	10.3	1	41.5	8.1
Carex pennsylvanica	2	17.1	8.4	2	23.9	10.3	2	13.6	7.6
Sanicula marylandica	3	9.4	5.5	4	3.5	5.7	3	9.6	7.6
Thalictrum dioicum	4	3.2	3.5	9	0.9	4.6	4	7.7	8.1
Heracleum lanatum	5	2.8	1.5		1.6	1.7		0.9	1.9
Anemone canadensis	6	2.6	2.0						
Aster sagittifolius	7	2.2	6.0	10	0.8	4.0	8	1.1	4.8
Osmorhiza claytoni	8	1.8	6.5						
Viola rugulosa	9	1.8	5.0		0.2	2.3		0.2	1.9
Maianthemum canadense	10	1.6	5.5	5	1.8	5.7	7	1.7	6.2
Taraxacum sp.		1.6	2.5		0.6	1.1		0.7	1.9
Rudbeckia laciniata		1.4	3.0		2.1	1.7	6	6.1	2.9
Fragaria virginiana		1.3	4.5	3	6.5	6.9	5	4.2	7.6
Total Herbage Cover, %		59.5			41.0			66.3	
Total Number of Species		40.0			39.0			39.0	

* Species with less than 1% relative cover in the unburned stand: *Galium boreale, Galium triflorum, Zizia aurea, Corylus cornuta, Pyrola asarifolia, Symphoricarpos occidentalis, Urtica dioica, Lysimachia ciliata, Nepeta cataria, Rubus pubescens, Vicia americana, Vitis* sp., *Arenaria lateriflora, Disporum trachycarpum, Fraxinus pennsylvanica, Ulmus americana, Acer negundo, Lathyrus venosus, Mentha arvensis, Oryzopsis asperifolia, Populus tremuloides, Prunus virginiana, Quercus macrocarpa, Ranunculus abortivus, Trillium cernuum, Viburnum edule,* Misc. Graminеae, *Osmorhiza longistylis, Lysimachia thyrsiflora, Smilacina stellata, Stachys palustris, Betula papyrifera, Pyrola secunda, Rosa acicularis.*

burned-over stands. This increase in the principal understory species occurred even though there was little or no total increase in foliage cover of herbs. There is no apparent significance to the depletion or addition of the species in the burned vs. the unburned stand. *Carex pennsylvanica* (Pennsylvania sedge) was second in relative cover in all 3 stands and *Sanicula marylandica* (black snakeroot) was either 3rd or 4th. These 3 species together averaged 63% of the herbaceous cover for the 3 stands.

In a discussion of the affinities of the North Dakota flora, Rudd (1951) pointed out the presence in the Turtle Mountains of species typical of the boreal coniferous forest, even though no coniferous species grow there today. Typical of this northern origin, or as remnants from a postglacial cool, moist northern coniferous forest, are the following species found in this study: *Cornus canadensis, Epilobium angustifolium, Pyrola asarifolia, Pyrola secunda, Rubus pubescens,* and *Viola rugulosa.*

The principal herbaceous dominant, *Aralia nudicaulis,* is a common understory of the mesophytic eastern deciduous forests. Other species typical of this forest are *Anemone canadensis, Maianthemum canadense, Osmorhiza Claytoni, Prenanthes alba, Pyrola asarifolia, Rudbeckia laciniata, and Trillium cernuum.* Several of these reach their westernmost limit in the Turtle Mountains where their existence is possible because of areas of moist, acid peat soils.

Soils

The soils of the Turtle Mountains are derived from a mantle of glacial till which was deposited over an isolated, eroded remnant of the Missouri Plateau. There are numerous low hills with intervening depressions which are small lakes, grassy meadows, or peat and muck areas representing beds of dried-up lakes or ponds. The mineral soils have an abundance of calcium and the areas studied varied in texture from clay to silt loam (Cobb 1917).

Comparisons of the effect on the soil of burning 72 yr ago and the succeeding changes in vegetational composition were based on the profiles and analyses of composite samples from 2 types of sites in each study area. In the Scully's Woods these included the crest of knolls and sites midway down a southern slope.

On the crest of the knolls there was no distinct difference in the litter, duff, and leafmold of the burned and unburned areas. Each stratum was about ½ in. thick. The A_1 horizon, however, was considerably thicker in the unburned stand—about ¾ in. as opposed to ¼ in. Animal burrows were more common in the unburned area in the A_1 and A_2 horizons. The latter stratum of a lighter grayish-tan color was deeper in the unburned area. The area subjected to severe ground fire would have lost its original organic horizons and left the A_1 horizon exposed to erosion. There was not a clear-cut line of charcoal deposit and

it is assumed that erosional forces on the crests completely removed this burned debris.

On the slopes of the knolls the organic layers were comparable in burned and unburned areas, but the A_1 horizon was deeper on the unburned area, being up to 4 in. deep in contrast to only ¼ in. deep on the burned area. The profile of the burned area showed a leached A_2 horizon which was not distinguishable on the burned area.

Laboratory analyses were made from composite samples taken from soil horizons in the several sites.

The most consistent contrast between burned and unburned areas was that of the soil pH of the upper horizons. The horizons of the burned Scully's Woods were consistently more acid, with contrasts of pH 5.6 vs. pH 6.8 in several equivalent horizons. These contrasts exist above the neutral layer rich in calcium, the B_{3ca} horizon. The total salt content as indicated by the conductivity of soil extract is slightly lower for the burned area and may be related to the increased leaching which has occurred with the increase in acidity on the burned areas.

Variations in organic carbon content below the A_1 horizon were not great. The A_1 horizon of the unburned slope was unusually low in organic carbon and that of the burned slope unusually high. The latter may be explained by an increase after the fire in herb cover, especially of grasses, which add a high content of fine, fibrous roots and easily humified shoots to the upper horizons. Also, charcoal left by the burn and eroded from above may have been incorporated into the A_1 horizon.

The profiles of burned and unburned sites indicate that the exchange capacity of the A_1 horizons reflects the organic carbon content, which is expected. Adding colloidal organic material to the mineral soil increases the cation capacity manyfold, so that it exceeds that of the best clay by 4 times or more.

The water-holding capacity of organic colloids is considerably higher than for mineral colloids; therefore, the A_1 horizons show a correlation of water-holding capacity and organic content.

Both cation exchange capacity and water-holding capacity in the B_1 horizons are influenced primarily by the percentage of clay content. Although the clay content varies, nearly all horizons have a sufficient mixture of clay, silt, and sand to be classified as loam, silt-loam, or clay-loam.

The soils of the Boundary Lake stand were not included in these comparisons because there was no unburned control stand. This area is relatively flat with poor drainage resulting from its low elevation between 2 lakes and from the heavy texture of the soil. Although the soils are classified as Rolla Silt Loam, most of the horizons are high in clay content with textures varying from silt loam to clay.

The soils of this stand present the most striking evidence of having been burned (Fig. 10). Below

FIG. 10. Soil profile of the clay soil of the Boundary Lake stand burned in 1886 and showing a 3 in. organic layer, the lower 1½ in. is mainly charcoal. Note the sharp transition to mineral soil.

the leaf fall of the current season is a 3 in. layer of decomposed litter, duff, and charcoal. The lower 1½ in. is composed of very fine black organic material in which are mixed fragments of charcoal up to ¾ in. in diameter. The line of demarcation between charcoal and mineral clay soil is unusually sharp. Apparently the surface fire was extremely hot and of a duration sufficient to completely burn the surface organic material. Subsequent leaching of the powdered charcoal has filled the cracks between the columnar structure and around soil aggregates, as shown in Figure 10 to the left of the ruler.

The intensity of the 1886 burn is illustrated by Figure 11. The A_1 horizon here was ¾-1 in. thick, with an A_2 horizon extending down to

FIG. 11. Soil profile at Boundary Lake showing charcoal layers from burned roots at 3½ and 5 in. (a and b), with a brick-tan, baked, clay layer (c) between. Soil structure below the charcoal is improved by the leached colloidal carbon.

about 4 in. To the right of the ruler at 3½ in. (a) and at 5 in. (b) are black areas, the lower one appearing as a nearly horizontal streak. These are areas of subterranean charcoal formed from the burning of tree roots. Between the burned roots is a layer of clay (c) about one inch thick which has been baked by the heat to a brick-like nature and brick-tan color. The charcoal from the roots has also had its effect on soil structure. From 4-5 in. below the burned roots the clay of the B_1 horizon has developed a subangular, blocky structure with fine films of charcoal leached downward. In contrast, the clay to either side and adjacent to the charcoal area is yellowish and poorly developed in structure, indicating the lack of lateral movement of colloidal material in heavy soils.

SUMMARY

This paper compares the present vegetation and soils of stands which were burned by a severe fire in 1886 with a control area which escaped at least severe burning. The locality is an outlier of the deciduous forest area in the Turtle Mountains of North Dakota on the U.S.-Canadian boundary. Principal trees are *Populus tremuloides, Quercus macrocarpa, Ulmus americana,* and *Fraxinus pennsylvanica.* Although pollen analyses of peat indicated conifers have been recently present, they were eliminated, probably by the lowering of water tables due to severe droughts and severe fires.

Vegetation was sampled by a modification of the arms-length rectangle method, using 100 plots of 0.01 acre size in each stand. Shrubs and small trees were sampled in $\frac{1}{250}$ acre circular plots and herbs and seedlings by 0.5×1M quadrats. Data were expressed as relative density, relative frequency, relative coverage, and importance percentage.

The unburned stand on undulating topography with soil developed from glacial till contained mature, straight-boled, forest-grown *Quercus macrocarpa* with trunk diameters of 19-26 in. and ages predating the 1886 fire. On nearby, unburned Masonic Island a 570 yr bur oak was over 36 in. dbh. Some *Populus tremuloides* occurred in the unburned stand with normal distribution in the size classes except for the unrepresented 3 in. class. This size class would require 20-24 yr of growth, the beginning of which would have been during the unfavorable drought years of the mid-thirties. *Fraxinus pennsylvanica* was most important in the 4-6 in. and the 10-12 in. dbh classes. *Betula papyrifera* was well represented in the various size classes but in fewer numbers than aspen and occurred principally along lake shores. The above four species made up 77% of the total density and 80% of the basal area. Principal understory trees were *Amelanchier alnifolia, Acer negundo, Prunus virginiana, Salix missouriensis,* and *Viburnum trilobum.*

An adjacent burned stand on similar topography and soil contained the same species of trees but their importance was different. *Quercus macrocarpa* was reduced from 2nd to 4th, *Ulmus americana* from 5th to 7th, and *Populus tremuloides* exceeded *Quercus* in importance percentage by 15 times. In the importance percentages by size classes, *Fraxinus pennsylvanica* exceeded the species in the 1-3 in. reproductive classes but *Populus tremuloides* excelled in other size classes. The highest percentage of *Quercus* trees was in the 4 in. dbh class, indicating the possibility of oak recovery under fire disclimax aspen cover. No mature *Quercus* occurred in the burned stand. The majority of *Populus* and *Betula* trees were in the 8 in. dbh class which would make them of an

age to have started growth just after the fire of 1886.

Following are the changes in relative density between unburned and burned stands: *Quercus macrocarpa* 16 to 3%, *Populus tremuloides* 38 to 70%, *Fraxinus pennsylvanica* 13 to 10%, and *Betula papyrifera* 10 to 6%. Relative basal areas changed as follows: *Quercus macrocarpa* 24 to 2%. *Populus tremuloides* 38 to 85%, *Fraxinus pennsylvanica* 8 to 3%, and *Betula papyrifera* 13 to 7%. The total density per acre was 465 with a basal area of 113 sq ft, nearly identical to the unburned stand.

A 3rd stand, typical of poorly drained clay soils and level topography, had been severely burned. *Populus tremuloides* was of greatest importance (67% density, 87% basal area) followed by *Salix missouriensis, Populus balsamifera,* and *Fraxinus pennsylvanica.* Large *Populus tremuloides,* up to 14 in. dbh, represented the first generation of regrowth from sprouts in areas where the root crowns survived. The total density of trees was 950 per acre, or double that of better drained sites. However, the basal area was only 97 sq ft per acre, or 81% of the other stands. Heavy soil and abundant moisture encouraged denser regrowth of aspen and willow.

There was little effect of the fire on foliage cover of shrubs after 72 years. *Corylus cornuta* dominated the shrub layer in all stands. The most obvious influence of the fire was a change in relative foliage cover of *Corylus* from 56% in the unburned stand to 80% in the burned stand. Although coniferous trees were lacking typical shrubs of the boreal forest were present. Most shrub species belonged to the drier deciduous woods and woodland-prairie margins. There were no species of strictly Rocky Mountain flora.

Herbaceous and seedling foliage cover in the 3 stands was very similar. Among species present only in the unburned stand were *Anemone canadense, Disporum trachycarpum,* and *Ranunculus abortivus.* The dominant herb in all stands, *Aralia nudicaulis,* was favored in the burned stand, increasing from 28% to 41% relative cover. Several typical coniferous understory species were probably remnants of a past coniferous forest.

The soils of the Turtle Mountains were derived from glacial till and vary from silt loam to clay. On both the crests of knolls and mid-slopes, the depth and organic content of the A_1 horizons were greater in the unburned sites. The most consistent contrast between equivalent horizons of unburned and burned sites was the greater acidity of the burned site.

The cation exchange capacity and water-holding capacity of the A_1 horizons was correlated to organic content which was highest in the unburned sites. In the B_1 horizons the above analyses were best correlated to clay content.

In places within the burned stand on clay soil there was a charcoal layer 1-2 in. thick below the more recent leafmold. Leaching of colloidal charcoal has filled cracks and surrounding soil aggregates. The intensity of burning was evidenced by charcoal remains of burned tree roots several inches below the surface with surrounding clay baked to a brick-tan color.

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THE EFFECT OF TEMPERATURE AND PHOTOPERIOD ON THE GROWTH OF *CARICA PAPAYA*

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Little is known about the natural distribution of *Carica papaya* L. beyond that it is believed to have originated in Central America. It has become naturalized in various locations in Hawaii, and is generally found in commercial plantings and home gardens below a thousand feet (Degener 1957), a generalization usually attributed to the temperature gradient. In commercial papaya areas of Hawaii, the average minimum temperatures seldom vary from 21° C and the average maximum from 26° C, nevertheless seasonal variation in germination and growth of *Carica papaya* can be easily observed. Went (1944, 1957) and others have shown that temperature plays a dominant role in the growth and reproduction of many plants with tropical habitats similar to papaya, but no previous work on the effect of temperature and photoperiod on germination and growth of papaya has been reported.

The purpose of this study was to measure some of the effects of day length and temperature on the germination of seeds and the growth of young papaya seedlings in order to better understand the responses of papaya to seasonal changes in the environment and how these changes relate to the natural distribution.

Materials and Methods

Germination

Seeds of ripe hermaphroditic Solo papaya (*Carica papaya* L.) were washed, cleaned of flesh, and the sarcotestae removed with a Waring blender at low speed. In the process of washing, seeds which floated were discarded. Fifty cleaned seeds were spread out on the surface of each of several 12-ounce metal containers filled with coarse vermiculite and covered with fine vermiculite. Each treatment was replicated four times with 50 seeds per replicate in the cans of vermiculite. Tap water was added as needed to keep the media moist.

Two series of germination experiments were conducted, one at the Hawaii Agricultural Experiment Station and another at the Pineapple Research Institute. Two constant temperature rooms at H.A.E.S., one with standard, cool, white, fluorescent lamps and a temperature of 26° ± 1° C, and other without lights and a temperature of 23° ± 1° C were employed. Also used were a seed germinator (35° ± 2° C), several thermostatically controlled ovens (45° ± 2° C, 40° ± 1°, 35° ± 1°, 30° ± 1°), and refrigerators (20° ±1°, 16° ± 1°, 12° ± 1° and 4° ± 1°). Night conditions were simulated by placing trays of planted seeds in these various chambers for night temperatures at 4 p.m. or 10 p.m. and returning them to the lighted control room at 8 a.m. for day temperatures.

The series of germination tests performed at Pineapple Research Institute were in two air-conditioned greenhouses and one greenhouse without temperature control. The temperature of one of the air-conditioned greenhouses was held at 27° ± 3° C by day and 16° ± 1° by night, whereas that of the other air-conditioned house was maintained at 38° ± 3° by day and 24° ± 1° by night. The temperature in the third greenhouse was 40° ± 4° by day and 24° ± 2° by night. Treatment changes were made at 8 a.m. and 4 p.m. daily; i.e., the day temperature was of 8 hours' duration and the night 16 hours. Higher than normal greenhouse temperatures were produced by clear plastic hotcaps with exhaust openings of different sizes. Percentage germination data were transformed to arc sin (Snedecor 1950) for analysis of variance and Duncan's (1955) multiple range test used to test significance.

Seedling Growth

The first seedling experiment was carried on at the Earhart Laboratory where papaya seeds were germinated in a 1:1 mixture of vermiculite and pea gravel at a 30° C. day-temperature and a 23° night-temperature. About one week following germination, the seedlings were transplanted into plastic cup containing the same medium. These transplanted seedlings were given Hoagland's complete nutrient solution three times weekly and grown at 26° C. days and 23° nights for twenty days, at the end of which time each cup was numbered and the heights of the plants measured. The plants were placed 12 to a truck.

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Treatments were as follows: 8 hours greenhouse light and 16 hours darkness at the following day/night centigrade temperatures: 23/17, 23/23, 26/20, 26/26, and 30/23. One month later their heights were measured and dry weights of the whole plants were taken. The data are presented as average centimeter increase in height per plant of 10 plants during the month and average dry weight of 10 plants after 9 weeks growth from seeding. The remaining seedling experiments were conducted in the temperature-controlled rooms and facilities at the Hawaii Agricultural Experiment Station described above under germination experiments. Each treatment consisted of 9 to 18 individual plants, randomly distributed under the lights in the 27° C. control room each morning.

Greenhouse plants were germinated and grown in metal cans (12 fluid ounces) containing coarse vermiculite with Hoagland's complete nutrient solution. When one to two months old, uniform plants were selected from a large excess and placed under the lights of the 26° C. control room for one week prior to treatment. Plants receiving variable night-temperatures were then transferred at 4 p.m. for the short day and 10 p.m. for the long day to the respective chambers for differential night-temperatures. At 8 a.m., all plants were returned to the control room where they received a 26° C. day of 1,000 foot candle intensity. Growth of the plants was excellent. After nineteen days of treatment, approximately two to three months from seed, plants were excised at the level of the most distal root. The top was measured and weighed fresh. Dry weights of the tops were also taken after being dried for 24 hours at 60° C. in a forced draft oven. The data were treated by the analysis of variance and Duncan's multiple range test was used to test the significance of the treatments.

Results and Discussion

Germination

Greenhouse observations and preliminary tests revealed that germination of papaya seeds was influenced by temperature but not by day length.

Photoperiod and Night Temperature on Germination.—Seeds germinated under different photoperiods but at a constant temperature of 26° C., showed no effect of day length *per se* (Table I). The rate of germination under 16 hours of light was the same as that under 8 hours. However, when seeds received a 26° day- and 16° night-temperature, no germination occurred until after 14 days. By 30 days after seeding, a lower per cent germination was found for those seeds receiving an 8-hour day, i.e., a long cold night (16 hours at 16°). These results appeared to stress temperature as an important limiting factor in germination of papaya seed.

Table I. The effect of day length and night-temperature on the mean per cent germination of *Carica papaya* l. seed at 14 and 30 days after sowing, at 26°C day and two night temperatures, 26° and 16°

Day Temperature	Night Temperature	Day Length	Per Cent Germination[1] After	
			14 Days	30 Days
Degrees C.	*Degrees C.*	*Hours*	*Per Cent*	*Per Cent*
26	26	16	24 b	78 b
26	26	8	33 b	90 b
26	16	16	0 a	82 b
26	16	8	0 a	53 a

[1] Mean values in a column with the same letter do not differ at the 5 per cent level of probability (2).

Night-Temperature and Germination.—When seeds were germinated during a simulated 8-hour day in a 35° C. germinator, changes in night-temperature produced marked effects on the per cent germination (Table II). After 8 cycles of night-temperatures below 26° C., there was a drop in germination from 68% to 27%. By 14 days, there was poorer germination at 16° C. than at 23° to 35° night-temperature. No explantation is available for the sudden increase in germination at 14 days with a 4° C. night; however, the relatively good germination after 14 days at the low night-temperatures of 4° and 16° support the necessity of high temperatures (35° C. day) sometimes during germination of papaya seed.

Table II. The effect of night-temperature on the mean per cent germination of *Carica papaya* seed growing in a 35°C. day and varying night-temperatures measured at 8 and 14 days after sowing

Day Temperature	Night Temperature	Per Cent Germination[1] After	
		8 Days	14 Days
Degrees C.	*Degrees C.*	*Per Cent*	*Per Cent*
35	35	62 c	78 b
35	26	68 c	78 b
35	23	27 b	81 b
35	16	0 a	44 a
35	4	0 a	74 b

[1] Mean values in a column with the same letter do not differ at the 5 per cent level of probability.

Numbers of Warm Nights and Germination.—When the seeds were germinated at 26° C. day-temperature and given various numbers of warm night (35°), the data again suggested a quantitative effect of heat (Fig. 1). The control (0

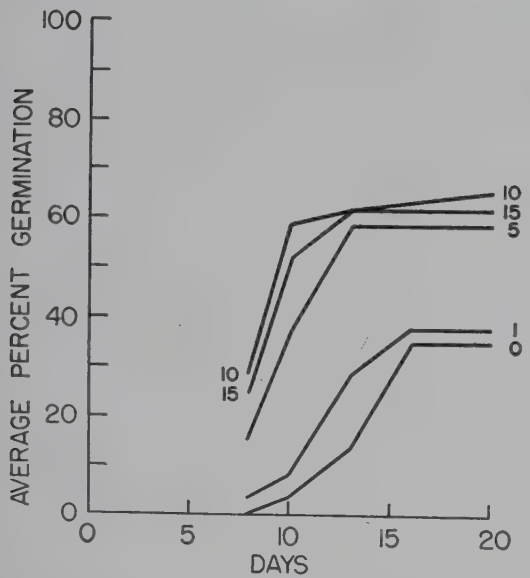


FIG. 1. The effect of the number of 35°C. nights (0, 1, 5, 10 and 15) on Line-8 Solo papaya seed germinating at 26°C. as measured at 8, 10, 13, 15 and 20 days after seeding.

nights at 35° C.) which received only 26° at night reached a maximum per cent germination after 16 days; whereas those seeds receiving five or more warm nights (35° C.) appeared to reach their maximum in fewer days and reach a higher average per cent germination than the control.

Greenhouse Temperatures and Germination.—When germinating papaya seeds were subjected to the varying day-temperatures in greenhouses, an average 24° C. night-temperature and 38° to 40° day-temperature appeared to be near optimum (Table III). Average night-temperatures of 16° reduced germination when compared to 24° night-temperatures. Temperature at 44° and above resulted in no germination.

Temperature Pretreatment of Seed and Germination.—In the previously discussed series of experiments high temperatures appeared to play a dominant role in the physiology of papaya seed germination. The mechanism by which germination was controlled by temperature was not apparent in this study, but one further step toward an explanation was developed in another series

TABLE IV. The effect of pretreating *Carica papaya* seed for 5 days at different controlled temperatures from 4°C. to 45°C on the mean per cent germination in a 35°C germinator measured at 10 days in three experiments

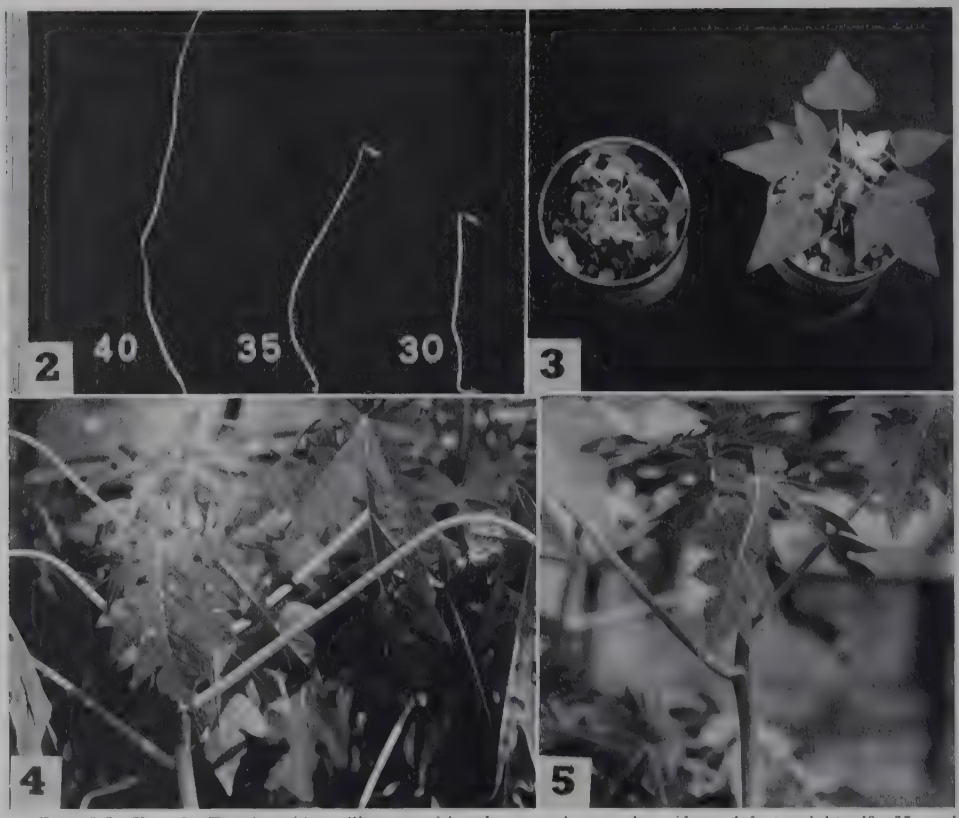
Pre-Germinator Temperature Treatment	Per Cent Germination After 10 Days at 35° C.		
Experiment	I[2]	II[2]	III[3]
Degrees Centigrade	*Per Cent*[1]	*Per Cent*[1]	*Per Cent*
1. Control (no pretreat.)	22 a	16 a	17
2. 45	—	48 c	39
3. 40	90 c	—	—
4. 35	61 b	31 b	—
5. 30	23 a	13 a	—
6. 16	0	—	—
7. 4	—	24 ab	—
LSD 05			11.8
01			15.4

[1] Mean values in a column with the same letter do not differ at the 5 per cent level of probability.
[2] Fresh cleaned seed from ripe fruit.
[3] Stored seed 10 months old when treated.

TABLE III. The effect of average greenhouse temperatures in an uncontrolled and a temperature-controlled greenhouse on germination of fresh *Carica papaya* seed as measured by the mean per cent germination after 12 to 22 days in three experiments conducted simultaneously

Average Temperature		Per Cent Germination[5] Counted After								
		12 Days			17 Days			22 Days		
8 am to 4 pm	4 pm to 8 am	Experiment I[1]	II[2]	III[3]	I[1]	II[2]	III[3]	I[1]	II[2]	III[3]
Degrees C.	*Degrees C.*	%	%	%	%	%	%	%	%	%
50[5]	24	—	0 a	—	—	0 a	—	—	0 a	—
45[5]	24	—	—	0 a	—	—	0 a	—	—	0 a
44[5]	24	—	—	0 a	—	—	0 a	—	—	0 a
40	24	—	17 b	—	—	82 c	—	—	82 c	—
40	16	—	0 a	—	—	1 a	—	—	29 b	—
38	24	36 b	—	25 b	66 d	—	50 b	74 c	—	57 b
38	16	0 a	—	—	54 c	—	—	72 c	—	—
33	24	—	—	36 b	—	—	53 b	—	—	59 b
27	24	0 a	0 a	—	30 b	18 b	—	42 b	32 b	—
27	16	0 a	—	—	0 a	—	—	0 a	—	—

[1] Experiment I—germinated in temperature-controlled greenhouses with low light intensity.
[2] Experiment II—germinated during the day in a greenhouse without temperature control under high light and control temperature at night except one treatment which was placed in 27° C. during day and transferred to 24° C. greenhouse at night.
[3] Experiment III—germinated in a greenhouse without temperature control under high light except one treatment which received 50 per cent shade (33/24).
[4] Plastic hot caps (with ventilation) placed in the greenhouse without temperature control.
[5] Mean values in any one column with the same letter do not differ at the 5 per cent level of probability.



FIGS. 2-5; FIG. 2. Ten-day-old seedlings resulting from seed treated at, from left to right, 40, 35, and 30°C. for five days before being placed in a germinator at 35°C. Note abnormal elongation caused by 40°C. treatment. FIG. 3. Comparison of two-month old papaya seedlings after 3 cycles of 26°/20°C. (left) and 26°/30°C. (right). Note the recurvature of petioles on the seedling which received the 4°C. night temperature. FIGS. 4-5. Comparison of a four month old papaya seedling 15 minutes after receiving a night of 4°C., (4) and control, i.e., 24°C. night (5).

of experiments in which seeds were pretreated for 5 days with different temperatures from 4° to 45° and then allowed to germinate at near optimum temperature of 35° (Table IV).

In preliminary tests not included in this report the effect of pretreatment with temperatures higher than 45° before being placed at 26° under lights was detrimental to seed germination. In three experiments pretreatment with temperatures of 35° to 45° for 5 days caused not only extreme etiolation of germinated seedlings (Fig. 2) but also a higher percent germination than among seeds not receiving pretreatment (Table IV). These results suggest the possibility that high temperatures up to a point may enhance germination by destruction of naturally occurring germination inhibitors in the seed coat of papaya (Lange 1961), as evidenced by the high per cent germination of preheated seed at only 10 days. The extreme elongation of seedlings was similar in appearance to growth responses to gibberellic acid.

Seedling growth

Effect of Night-Temperature Versus Day-temperature on Seedling Growth.—The height of young papaya seedlings growing under controlled conditions was more dependent on night-temperature than on changes in the day-temperature (Table V). Plants grown at a constant 26° C. day and 26° night-temperature increased nearly twice the amount of those grown at a 26° day and 20° night. The average increase in height per plant at 26° night-temperature was 7.59 cm as compared to 5.04 cm at 23° and 3.83 cm at 20°. With a constant night-temperature of 23°, a

TABLE V. The effect of day and night-temperature on the growth of young *Carica papaya* L. seedlings as measured by mean dry weight and increase in height per plant after one month of treatment (age nine weeks at harvest). Photoperiod was from 8 am to 4 pm

Day Temperature	Night-Temperatures							
	26° C.		23° C.		20° C.		17° C.	
	Height[1]	Weight[2]	Height[1]	Weight[2]	Height[1]	Weight[2]	Height[1]	Weight[2]
Degrees C.	*cm*	*gm*	*cm*	*gm*	*cm*	*gm*	*cm*	*gm*
30	—	—	4.79 c	.161 x	—	—	—	—
26	7.59 d	.281 y	5.04 c	.281 y	3.83 b	.240 y		
23	—	—	4.57 c	.240 y	—	—	2.78 a	.161 x

[1] Means for all heights followed by the same letter do not differ significantly at the 5 per cent level of probability.
[2] Means for all dry weights followed by the same letter do not differ significantly at the 5 per cent level of probability.

TABLE VI. The effect of 19 cycles day length and night-temperature on the mean height and dry weight of tops of *Carica papaya* seedlings growing at a constant 26°C. day as measured at 14 weeks of age in two experiments

Night Temperature	Long Day				Short Day			
	Height		Weight		Height		Weight	
Experiment	I[1]	II[2]	I[1]	II[2]	I[1]	II[2]	I[1]	II[2]
	cms	*cms*	*gms*	*gms*	*cms*	*cms*	*gms*	*gms*
10° C.	—	10.47 b	—	0.353 cd	—	9.04 a	—	0.179 a
16° C.	9.39 a	10.66 bc	0.289 bc	0.313 c	9.88 ab	11.61 de	0.193 a	0.243 b
26° C.	10.13 bc	11.41 cd	0.318 c	0.387 d	10.89 c	12.26 e	0.254 b	0.321 cd

[1] Means for the height and weight columns in Experiment I followed by the same letter do not differ significantly at the 5 per cent level of probability.
[2] Means for the height and weight columns in Experiment II followed by the same letter do not differ significantly at the 5 per cent level of probability.

change in day-temperature, 23° to 30°, had no significant effect on height.

The greatest increase in average dry weight per papaya seedlings occurred in a regime of 23° to 26° day with a 20° to 26° night. Although there appeared to be no significant effect of night-temperature above 17° C. in the average increase in dry weight, there appeared to be significantly less dry weight resulting from a 30° day and 23° night-temperature (Table V).

Effect of Photoperiod and Night-Temperature on Seedling Growth.—There appeared to be effects of photoperiod on the growth of papaya seedlings in two experiments (Table VI). In Experiment II at 10° C., the height of papayas growing during long cool nights (short day) was less than those growing in short cool nights (long day); whereas at 16° and 26° the effect of day length was reversed so that maximum height was attained during a long warm night (short day, 26° C.). Seedling height was consistently dependent on temperature, i.e., the higher the temperature, the greater the average height at both long and short day.

Average dry weight was consistently greater for plants receiving a long photoperiod regardless of night-temperature. Dry weight tended to increase with night-temperature up to 26° when grown in short days but did not show significant differences during long days.

The Effect of Night-Temperature on Seedling Growth.—Young papaya seedlings grown under controlled conditions of 26° by day and varying night-temperature grew most rapidly near 26° C. to 30° C. nights (Table VII). The night temperature requirement for maximum fresh and dry weight tended to be somewhat lower than for maximum height, i.e., nearer 23° C. to 30° C. Maximum height and weight varied from experiment to experiment which may have been due to the use of slightly different age plants, i.e., eight to twelve weeks. This age papaya seedling represents a size close to that used for transplanting into the field and is an age during which the plants undergo rapid growth and are presumably highly sensitive to changes in the environment. In nature, papaya plants tend to grow tall and slender during high night-temperatures or under shady conditions.

In the preceding experiments a striking visual response of papaya seedlings to low night-temperatures was apparent from the recurvature of the petioles at night-temperatures below 20° C. similar to a "sleep effect" of beans or a mild hormone response (Fig. 3). The abnormal bending of the petioles occurred after only a few hours

TABLE VII. The effect of night-temperature on the average height, fresh weight and dry weight of *Carica papaya* seedling tops after 19 days while growing at 26°C day and night-temperatures from 4° to 40° with an eight-hour day in three experiments

Night Temp.	HEIGHT			FRESH WEIGHT			DRY WEIGHT		
Experiment	I[1]	II[2]	III[3]	I[1]	II[2]	III[3]	I[1]	II[2]	III[3]
	cms	*cms*	*cms*	*gms*	*gms*	*gms*	*gms*	*gms*	*gms*
4° C.	—	7.0 a	9.4 a	—	0.82 a	1.30 a	—	0.099 a	0.122 a
12° C.	—	—	10.1 ab	—	—	1.43 ab	—	—	0.137 a
17° C.	9.0 b	9.0 b	10.2 ab	1.19 c	1.57 b	1.65 bc	0.133 c	0.186 b	0.194 b
20° C.	—	9.5 b	10.8 bc	—	1.67 b	1.81 cd	—	0.195 b	0.201 b
23° C.	9.8 c	10.2 bc	11.7 cd	1.45 c	1.81 b	1.92 d	0.150 c	0.215 b	0.222 b
26° C.	10.2 c	10.9 c	12.0 d	1.29 c	1.80 b	2.20 e	0.134 c	0.198 b	0.210 b
30° C.	11.1 d	12.4 d	—	1.32 c	2.28 c	—	0.127 c	0.225 b	—
35° C.	9.9 c	—	—	0.85 b	—	—	0.084 b	—	—
40° C.	8.3 a	—	—	0.52 a	—	—	0.046 a	—	—

[1] Age 8 weeks from seeding.
[2] Age 10 weeks from seeding.
[3] Age 12 weeks from seeding.
Means for each column followed by the same letter do not differ significantly at the 5 per cent level of probability.

of cool temperature. It was also observed that plants recovered to normal petiole form more rapidly after having been treated with 17° C. than at 12° or 4° night-temperatures. The intensity of petiole response appeared to decrease with age. In other experiments not fully described here, four-month-old plants showed curvature only after receiving temperatures of 4° C. (Fig. 5), whereas month-old seedlings showed petiole curvature below 26° night.

The optimum night temperature for rapid seedling growth under the condition of these experiments appeared to be between 26° and 30° C. for height and between 17° and 30° for weight. Although there appeared to be no significant difference between weights above 17° night temperature in three experiments, there was a consistent trend for weights to be higher at temperatures above 17° nights. The annual average temperature in Honolulu was reported (Weather Bureau 1958) at 24° with an average maximum of 26° and 21° minimum. The average monthly temperature in January, February and March may drop to a 24° day and 19° night; whereas the average summer temperatures in July, August and September are more optimum for papaya growth, i.e., 28° day and 23° night.

The results of these experiments may in part suggest the reasons for reduced rate of germination and growth of young seedlings during winter months in Hawaii and at other locations in the world too cool for optimum growth of papaya.

SUMMARY

Carica papaya L. seeds and seedlings were cultured under conditions of controlled light and temperature for short periods of time. Seed germination was temperature-dependent, showing an optimum temperature near 35° C. Temperatures below 23° and above 44° were deterimental to germination. Night-temperature appeared to be more critical for seedling growth than day-temperature or day length. Photoperiodic effects appeared to be interrelated with night-temperature. Optimum night-temperature for dry weight increases was between 17° C. and 30° whereas maximum seedling elongation occurred near 30° night-temperature when plants were grown at 26° day-temperature and eight-hour photoperiod.

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THE BIOLOGY OF *DESMANTHUS ILLINOENSIS*[1]

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INTRODUCTION

Desmanthus illinoensis (Michaux) MacMillan is an herbaceous or suffrutescent perennial legume of wide but sparse distribution throughout the midwestern and southeastern U. S. It occurs rather commonly along roadside ditches, at the margins of cultivated fields, in upland swales and on low, open ground. Leaves are twice pinnate and consist of many small, linear leaflets. The numerous dense heads of small, white flowers are borne on axillary peduncles. Flowering begins in late May and early June and may continue into the summer, with both flower buds and bundles of mature, strongly curving capsules occurring on the same plant.

This study of *Desmanthus illinoensis* was undertaken to describe some of the autecological and biological aspects of the species, which has been little investigated from any other than a taxonomic viewpoint. In addition, it is a prairie forb apparently favored by livestock in grazing and thus merits study on the basis of its potential economic value.

Data were assembled during the spring and summer of 1957 and 1958 from material observed within a 10 mile radius of Tulsa, Okla. Some of the data was compiled during the spring and fall of 1958 from laboratory plantings at the Agricultural Experiment Station at the Univ. of Cal., Los Angeles.

CLASSIFICATION AND DISTRIBUTION

The genus *Desmanthus,* of the subfamily Mimosoideae of the Leguminosae, is native to the New World and consists of some 30 species, the majority of which are native to Mexico and Central America. *D. illinoensis* has in the past been placed in both the genus *Acacia* and the genus *Mimosa,* attesting to the close relationship of the 3 groups. It is the only *Desmanthus* species other than *D. leptolobus* distinguished by 5 stamens, and differs from *D. leptolobus* in its greater number of flowers per head and smaller, curving legumes.

D. illinoensis is the most widely distributed of *Desmanthus* species in the U. S. It ranges southward from S. D. and Minn. through Colo., N. M. and Texas, and eastward to Ohio, Ken., Tenn., the Carolinas and into Fla. The great diversity of habitats in which it is found indicates a wide temperature and moisture tolerance.

ECOLOGY

The region of the field studies is predominantly tall grass prairie, with floodplain forest bordering the streams and post oak-black jack forest crowning the hills. This prairie is part of a southerly extension of the tall grass prairie association which reaches climax development in Kan. and farther west in Okla. The area lies between the oak-hickory deciduous forest covering the Ozark Mountains to the east and the oak-hickory savannah of the Sandstone Hills to the west. It is traversed from northwest to southeast by the Arkansas River and several of its smaller tributaries. Average annual precipitation is 32 in. and the average annual temperature is 61° F.

The soils of Tulsa County are of wide diversity due to the several kinds of parent rock materials and the high overflow deposits of the Arkansas River. However, soil acidity or alkalinity is apparently not a significant edaphic factor in the distribution of *D. illinoensis,* as stands are found in more or less equal abundance on sandstone or limestone substratum.

In the study area, *D. illinoensis* occurs in small, scattered stands along railroad rights-of-way, roadsides, the margins of cultivated fields and in uncultivated fields which are undisturbed by grazing. In areas of uneven topography, it is in swales where there is more abundant moisture. The stands, though small in area, are usually dense and the individual plants are in close proximity. Vacant city lots which are relatively undisturbed except for one or 2 high mowings per year are common habitats. One plant with mature fruits was observed in a downtown industrial area growing in a crack between a concrete wall and the sidewalk. There was no open ground within a block of this hardy individual.

D. illinoensis is a minor forb of the tall grass association. Its associates are the dominant

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grasses of the tall grass prairie: *Andropogon scoparius* Michx., *A. gerardi* Vitman, *Panicum virgatum* L. and *Sorghastrum nutans* (L.) Nash, and the usual grasses and forbs of the prairie community.

Insect Parasites

Insect collections from *D. illinoensis* made at intervals during the summers of 1957 and 1958 were sent to the Entomology Research Division of the U. S. D. A. at Beltsville, Md., for identification. In the late summer of 1957 seed heads were heavily infested with larvae and adults of a small beetle of the family Bruchidae, Order Coleoptera. The adults of this family are typically short and stout; the larvae are grublike and almost legless, living inside legume seeds (Little 1957). It is a relatively small family but contains several species of considerable economic importance as pests in various kinds of stored peas and beans. The bruchids were a species of *Acanthoscelides* and are apparently new to the U. S. Seed loss by the bruchid infestation was quite heavy. The larvae were within the seeds, a single larva fitting snugly within each seed case. Both larvae and adults were found in large numbers at several collecting places in 1957. In 1958 only a few adult bruchids were collected from *D. illinoensis*. No others were observed in the field.

In June, 1958, swarms of a chrysomelid beetle, *Anomoea laticlavia* (Forst.), fed on young vegetative and flowering parts of *D. illinoensis* at several locations. The Chrysomelidae, Order Coleoptera, is a family of foliage feeders closely related to the Bruchidae. Most chrysomelids disappeared after a few weeks but they had heavily damaged the terminal portions of the plants. Lateral branches produced flower buds later in the summer but many did not mature and there was little seed set.

The third most abundant insect was *Lachesilla nibilis* (Aaron) of the family Lachesillidae (Psocidae), order Corrodentia. This group of small insects, which also includes booklice, feed upon dry vegetable matter. The lachesillids were found during the late summer of 1957 among the dry seed heads. They probably fed on the dried leaves and seed capsules. They were not observed during the summer of 1958.

Other insects (from 1 to 8 specimens each) collected in 1957 from *D. illinoensis* were: *Phyllobaenus sp.* (scabra ?) (Cleridae, Coleoptera); *Melanophthalama* sp. (Lathridiidae, Coleoptera); *Blissus leucopterus* (Lygaeidae, Hemiptera); species of Noctuidae (Lepidoptera); and species of Collembola.

Bacteria

D. illinoensis roots are moderately nodulated by *Rhizobium* bacteria. According to Dr. Lynn Gee, Department of Bacteriology, Okla. State Univ. (personal communication 1958), the work of Dr. J. K. Wilson at Cornell Univ. is most comprehensive in this area and indicates that *Rhizobium* species isolated from *D. illinoensis* will nodulate the following Leguminosae: *Caragana frutescens, Crotalaria spectabilis, Desmodium canadense, Sesbania macrocarpa, Swainsonia coronillaefolia,* and *Vigna sinensis.*

Grazing and Mowing Effects

D. illinoensis is preferentially grazed by cattle as strikingly shown in a field stand observed in the summer of 1957. It had not been cultivated and the natural grasses had been maintained for grazing. The fine stand of *D. illinoensis* occupied approximately 3 acres on a north-facing slope between the knolls of the hill. In September, 1957, the season's leaves had dried and fallen, leaving the upright, drying stems and an abundance of seed heads (Fig. 1). One year later not a single stalk was evident.

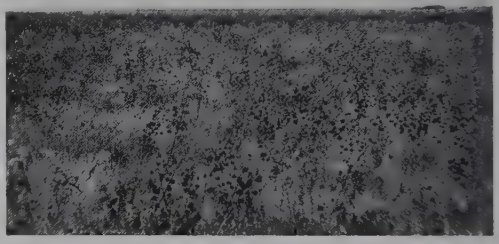

Fig. 1. Ungrazed field stand of *Desmanthus illinoensis* showing numerous stalks covered with brown seed heads.

No cattle had been in this field for at least 3 yr. A herd was moved in during the spring of 1958 and allowed to graze at will through the growing season. By June 24 many plants of *D. illinoensis* had begun growth and were well developed, but were eaten back to an 8-16 in. level by the cattle. New lateral growth had begun, but this, too, was grazed later.

In contrast to this, stands of *D. illinoensis* along roadsides and railroad rights-of-way are mowed once or more each summer and apparently benefit from this, becoming fuller in form and flowering throughout the summer.

Temperature and Day Length Response

To determine the growth response of *D. illinoensis* at varying temperatures, 3 groups of seedlings were placed in greenhouses at 50°, 60° and 65° F (night temperature), respectively. Maximum day temperatures in the greenhouses were 87°-88° F. A fourth group was placed outdoors, where minimum temperatures were 51° F ± 4° and maximum temperatures were 69° F ± 4°. Average dry weights of the different groups were lowest in the outdoor plants, increasing in those plants at 50° and 60° F, and were greatest in those at 65° F. Average dry weights varied from 1.99 g in the outdoor plants to 3.59 g in the 65° F house plants. Although the greenhouse plants were taller and heavier, the main stems had few axillary branches and tended to straggle. The outdoor control plants were small, with sturdy stems and some axillary branching. These differences in growth were apparently due to both light and temperature factors. All plants outdoors contained abundant anthocyanin in the new leaf growth, glands, petioles and stems. Plants in the greenhouses showed no obvious pigmentation.

To determine the response to day length, short days of 9 hr were given one group of seedlings by shading with black cloth, and long days were given another group by lighting with Mazda bulbs of 10-20 ft candles for 4 hr during the night. All plants were in outdoor benches. Duration of the experiment was from April 4 to June 11, 1958.

The response to long and short day treatments, although expected since *D. illinoensis* is a summer-blooming plant, was striking. The development of short day plants was very slow and hardly measurable toward the end of the study. Plants remained short, with little increase in leaf number. Leaves were small and almost no axillary buds formed. The long day plants were tall, full-foliaged with sturdy stems, branches, large leaves and many axillary buds. Flowering did not occur before the experiment was terminated.

Morphology

Seeds

The small, shining, brown seeds of *D. illinoensis* are flattened, somewhat triangular in outline and average 4 × 3 mm in size. The seed capsules are beaked and strongly curved, spiralling around the receptacle. Number of seeds per capsule varies from one to 7; the usual number is 5. About half the capsules from which the seed counts were made contained at least one undeveloped seed, and less than one-fifth contained 2 or 3 undeveloped seeds. Seeds are most easily germinated as soon as they reach maturity, a considerable seed coat impermeability developing with age. Evidence for the decreasing permeability of the seed coat is indicated in the following tests:

Mature seeds collected on July 11, 1958, from a plant whose flowers had first bloomed one month earlier were placed in Petri dishes between moist filter papers. Within 3 days 83% had germinated.

Seeds collected in September, 1957, at least 7 weeks after flowering, were stored at room temperature for 4 months and then placed between moist paper towels. After 5 days only 9% germination was obtained.

To determine the conditions under which the seeds most readily germinate, 5 different treatments, using 200 seeds for each, were given. The seeds were about 6 or 7 months old. Treatments were: 1) Alternate freezing and thawing—4 consecutive times; 2) Hot water—immersion in water at a little less than boiling temperature, then soaking for 3 hr as the water cooled; 3) Sulfuric acid— seeds placed in concentrated H_2SO_4 for 10 min, removed to note that only the outer seed coat was dissolved, then returned to the acid for 7 min, until the inner seed coat became softened or broken; and 4) Scarification—seeds clipped at end opposite micropyle with a knife, cutting through the seed coat.

The percentage germination following these treatments were: alternate freezing and thawing, 7%; hot water, 2½%; sulfuric acid, 76%; scarification, 97%; and control, 18%.

In 2 other tests lots of 40 and 44 seeds were pricked by inserting a needle through the seed coat. All seeds were placed in Petri dishes between moist paper towels. One hundred per cent germination was obtained within 24-48 hr from both lots of pricked seeds. None of the control seeds germinated within that time.

Treatments with various fat solvents were effective aids to germination, indicating the presence of the fat derivatives, suberin and cutin, in the seed coat.

A test of duration of viability was made of 2 yr old seeds. Seeds from the 1957 crop were clipped with a knife, then placed in a Petri dish between moist towels. In 24-48 hr 90% had germinated and the remaining 10% were swollen.

Seed capsules usually rupture after maturation, spilling seeds on the ground. However, many capsules do not open completely and seeds are retained within the capsule on the stalk for some

time. A monthly count over 6 months showed that the average number of seeds per head decreased from 17 the first month (January) to 3 the last month (June).

Seedlings

Seedlings were observed in the field as early as April 22 and also in mid-summer. Developmental rate of seedling growth appears uniform. In laboratory seedlings, the cotyledons, which are the size of the enclosing seed coat, enlarge for about 10 days. The maximum size was 7×5 mm. They remain green for about 2 wk, after which they begin to wither and eventually drop.

In germination, the 2 cotyledons are lifted above the soil surface. In some instances the seed coat still encircled the cotyledons, and unless it ruptured, allowing the cotyledons to expand, seedling growth was cut off. This was not observed in nature, but surely occurs.

Laboratory seedlings were used to determine the growth pattern of the leaves and pinnae. This was observed through the 27th leaf and was essentially the same in all plants. The first leaf above the cotyledons is only once pinnate and consists of either 4 or 5 pairs of leaflets. The second and all other leaves are doubly pinnate. Pinnae are usually an even number, but an occasional odd number was observed. This was also true of pinnae leaflets. The leaf development pattern is revealed in the first 10 leaves, with pinnae pairs increasing about every 2 leaves and gradually adding additional leaflets. The pattern is maintained to the 18th leaf, then pinnae and leaflet increase slows, and by the time the 27th leaf develops the number of pinnae remains at a variable 10-14 pairs with leaflet pairs ranging from 13-26.

Mature plants in the field had leaves with from 9-15 pinnae pairs, and up to 31 leaflet pairs in the middle part of the pinna. It therefore seems that leaves have attained a mature aspect after the development of 25-30 leaves and that succeeding leaves differ only in size. Average size of the mature leaf is about 8×4.5 cm. The average pinna is 30×4 mm, and the leaflets are about 3×1 mm.

New growth of the seedlings shows a definite pigmentation which is not evident on mature plants except when the seed capsules are reaching maturity. At that time the capsules become rosy-red, then dark red and finally brown. The rosy-red color is seen at the apex of the seedling, in the axillary branch buds, leaf petioles and petiolar glands.

Vegetative Body

Stems

Classified according to Raunkaierian life-form, *D. illinoensis* is a hemi-cryptophyte, the aerial body consisting of 2-6 stems which have risen from perennating buds just below the soil surface. The stems are loosely spreading and somewhat lax in habit, forming an open crown. The plant varies in height from ⅔ to 2m; the average height is from one to 1⅓ m.

Roots

The root system develops rapidly and becomes extensive early in the life of the plant. It is quite large even when the top growth is still relatively small. Then, corky layers are quickly formed on young roots and contain large numbers of lenticels which appear on the root surface as small, white, cottony protrusions. With increased age the roots become woody and tough.

Leaves

Leaves are dark green, which makes them slightly more conspicuous than their neighbors of lighter hue in the field. Leaflets exhibit the diurnal closing phenomenon common to many Leguminosae. In *D. illinoensis* it is believed to be influenced by some factor other than light, as leaflets closed early (around 4:00 PM) and opened before daylight (about 5:00 AM). They are not sensitive to touch. Cotyledons also exhibit diurnal closing.

Stomatal counts were made on leaflets from plants in 6 different locations. Stomata on the upper surface were consistently concentrated toward the leaf tip, averaging 149/sq. mm at the tip, 85 at the center and 51 at the base. The reverse was true on the lower surface of the leaflets, which contained a much larger number of stomata. There was an average of 265/sq. mm at the tip, 303 at the center and 351 at the base.

From one to 13 flat, circular, yellow glands, about 0.5 mm in diameter, dot the leaf rachis at irregular intervals.

The lower parts of the stems and branches are leafless, as the older leaves do not persist long. In the late summer, after the seeds are mature and the capsules brown, most of the remaining leaves dry and drop before those of surrounding vegetation. The bare stalks and brown fruits are then conspicuous among the prairie community.

Reproduction

In the summer of 1957 there was an abundance of seeds, even though many had been parasitized by bruchids. There was also abundant rainfall

in the spring of 1957 (April—8.74 in., in May 9.80 in., according to records of the U. S. Weather Bureau, Tulsa Municipal Airport). In 1958, flower buds were plentiful, but there was little fruit development. Many buds did not mature but aborted on the plant. The rainfall in the spring of 1958 was considerably less (April—4.36 in., May 3.69 in.) than that of 1957, and a direct correlation of moisture and flower development with subsequent seed set is suggested. Since 1957 was a year of unusually high rainfall and 1958 approached the average, it appears that seed production is normally low. Because of the low percentage of germination under conditions most closely approaching those in nature, propagation by reseeding is probably not the chief means of maintaining the species, even though it may be the principal method of increased distribution. The plants perpetuate by overwintering buds which are just below the soil surface at the base of the current season's growth. It is not known how long an individual plant may persist, although one root showed 6 annual rings.

Inflorescence

The small, round heads of white flowers are borne on upright, axillary peduncles which vary from 2-5 cm in length and are strongly angled. In a season of ample rainfall the flower heads occur in the axils of almost every leaf, although many abort. Flowers are spirally arranged on the slightly elongate receptacle.

In bud, the stamens and style are crumpled in apparently haphazard fashion within the upper part of the petals, which are neatly and symmetrically joined, converging at the apices. The anthers fall within a few hours after the flower opens, and the filaments straighten, giving the head its characteristic fuzzy appearance (Fig. 2).

Fig. 2. Flowering head of *D. illinoensis*. In bud (left), fully opened (right).

The slender, flat, white filaments are 5-6 mm long; anthers are 2 locular with longitudinal dehiscence. There are commonly 5 stamens, but in many instances one to 3 additional stamens, or, more usually, staminodes, were observed. The unilocular ovary, about one mm long, is slightly curved and strongly beaked even in the early flowering stage. The style is 5½ mm long, topped by the slightly enlarged stigmatic surface. The tubular calyx, 2 mm or less long, encloses 5 greenish white, straplike petals about 3 mm long.

The average number of flowers per head was determined by collecting 20 heads at random from each of 3 different stands located several miles apart. The averages were 49, 51 and 52. The lowest number of flowers on a head was 29 and the highest was 82. The full flower head measures from 7-9 mm across.

A similar determination was made with 20 heads collected from each of 3 different locations to see how many ovaries developed into fruits on each flower head. The averages were 31, 41 and 41. The lowest number of fruits on a head was 16 and the highest was 63.

Anatomy

In the young seedling there is an obvious collar, or flange, midway on the hypocotylary axis. As the seedling matures, the flange marks a definite external change between root and stem, the axis below the flange becomes brown and corky, the axis above it becomes green and is slightly smaller in diameter. Internally, the flange level marks the vascular transition zone.

Transverse sections show young root tissues to consist of epidermis, cortex, endodermis, pericycle and vascular tissues. The xylem tissue is tetrarch and the xylem transition pattern is one commonly found with this arrangement. With maturity, a thin, heavily suberized, corky bark replaces the epidermis and a band of thick-walled sclerenchyma fibers is built up in the phloem tissue, persisting over several years. Spring and late summer wood are easily distinguished.

Transverse section of a leaflet shows an epidermis one cell thick, a single palisade layer, spongy chlorenchyma and a single vascular strand extending longitudinally through the leaflet. Total thickness of the leaflet is about 8 cells.

Stem tissue consists of a two-layered epidermis with a thick cuticle, a narrow cortical layer of chlorenchyma and collenchyma, vascular tissue and a narrow pith zone around the central hollow cylinder. In the phloem tissue, there is a lacunar layer which appears to be formed by the breakdown of primary phloem.

Phenology

During the spring and summer of 1958, notes were made on the seasonal growth development. Spring growth began the latter part of April, vegetative bud development being observed on April 20. Vegetative growth increased through May and June. The last week of June flower buds appeared. Plants were marked at 5 different locations to follow the development of buds through flowering and fruit maturation. Thirty-nine buds were observed through the flowering stage. Of these, 23 of the flower heads reached full maturity. The remainder were victims of insect feeding or roadside mowing, or did not develop.

Cross-pollination by wind may occur but self-fertilization is probable. As evidence for self-fertilization, an isolated greenhouse plant flowered and set seed.

Flowering occurred 8-20 days after the buds were observed; the average number of days was 14. The flowers dried and turned brown within 2 days. By mid-July plants were in full bloom; however, many flower buds aborted, possibly due to insufficient moisture. The ripening ovaries remained flat as they increased in size, becoming full and rounded when mature. The capsules were at first shiny green, then red, darkening and becoming dull and granular in appearance. This was considered the time when the seeds were mature. The pods then shrank with drying, turned brown and usually dehisced. The seeds are probably mature from 7-10 days before the capsule opens. Fruit capsules browned and split open from 23-30 days after flowering, or an average of 27 days from flowering to full maturity.

By mid-August, the seasonal cycle was almost complete. Exceptions were those roadside plants which had been mowed and subsequently produced new lateral growth with abundant flowering.

Summary

This study describes some of the autecological and biological aspects of *Desmanthus illinoensis*, a perennial herb of the subfamily Mimosoideae of the Leguminosae, and a minor forb of the tall grass prairie association. The chiefly tropical genus is native to the New World, with some 30 species, of which *D. illinoensis* is the most widely distributed in the U. S.

Vegetation of the study area near Tulsa, Okla., is typical prairie and oak-hickory savannah. Plant associates of *D. illinoensis* include the dominant grasses of the tall grass prairie and the other grasses and forbs of the prairie community.

D. illinoensis occurs in small dense stands in dips and swales, and along railroad rights-of-way and roadsides. It is found on both acidic and alkaline soils.

The three most abundant insect parasites were 1) a species of *Acanthoscelides*, a small beetle (family Bruchidae) apparently new to the U. S., the larvae of which were found within the seed cases; 2) the chrysomelid beetle *Anomoea laticlavia* (Forst.), a foliage feeder, and 3) *Lachesilla nibilis* (Aaron), family Lachesillidae, order Corrodentia, a feeder on dry vegetable matter.

D. illinoensis roots are moderately nodulated by *Rhizobium* bacteria.

Heavy grazing causes the almost complete disappearance of *D. illinoensis* but light mowing is beneficial, resulting in greater vegetative growth and a longer flowering period.

Experiments showed seedling development to be negligible under short day treatment, while seedlings given long day treatment developed rapidly into tall, full-foliaged sturdy plants.

Seed germination tests showed no dormancy period. Natural germination percentage is low due to the decreasing permeability of the seed coat with age. Clipping or pricking of the seed coat usually results in 97-100% germination.

Vegetative development of the seedling follows a distinct growth pattern, assuming a mature aspect when 25-30 leaves have developed. The vegetative body, about one meter high, consists of 2-6 ridged stems with bipinnate leaves with 10-14 pinnae pairs each with 13-31 leaflet pairs. An average of 50 flowers occur in small, dense heads borne on axillary peduncles. An average of 37 ovaries develop into fruit capsules. Flower and seed loss is great due to insufficient moisture and/or insect depredations. Apparently reproduction is chiefly by means of overwintering buds.

Root vascular tissue is tetrarch and the transition to stem structure follows a pattern common in such an arrangement. The occurrence of a flange at the intermediate level is an unusual feature. Both root and stem have large amounts of sclerenchyma. The stem is hollow, with collateral vascular bundles.

Spring growth in the study area begins in late April. Vegetative growth progresses for 6-8 wk; time from bud formation to flowering is about 2 wk; time from flowering to mature fruit is about 4 wk.

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PATTERN IN PONDEROSA PINE FORESTS

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The ponderosa pine (*Pinus ponderosa* Laws.) forests of northern Arizona, although relatively simple in species composition, have a complex spatial structure. At least 4 distinct scales of pattern can be identified: a large scale pattern induced by local variations in topography and soils; a mosaic of even-aged groups, averaging about ⅕ acre in size; variability in stand density within an even-aged group; and the arrangement of the individual trees making up a uniform stand.

The ponderosa pine forests of southwestern United States are particularly suitable for the study of spatial and temporal patterns in plant communities. In most of the region, ponderosa pine is not only the dominant, it is virtually the only tree in the forest. Relatively few age classes are represented, for only in the occasional years when a good seed crop and favorable moisture conditions coincide can abundant reproduction become established. Several features of the environment and of the life history of the species reinforce the tendency toward pattern formation that is perhaps normal in any plant community.

Field work for this study was carried out during the summer and fall of 1957 on the Fort Apache Indian Reservation in east central Arizona. Thanks are due to the Tribal Council of the White Mountain Apache Tribe for permitting collection of field data on their tribal lands. Financial support was provided in part by the National Science Foundation through the Botany Department at Duke University. I am grateful to Dr. J. Roger Bray for his comments on the manuscript.

TYPES OF PATTERN IN PONDEROSA PINE FORESTS

The largest observable scale of pattern results from local variations in elevation, topography, and soils. Minor differences in stand density, tree growth, and understory vegetation often accompany relatively slight changes in slope, aspect, or soil depth. These patterns and their correlation with environment have long been studied by ecologists. The influence of climate and soil on the vegetation of southwestern forests has been

well summarized by Pearson (1931), and will not be discussed in detail here.

Within a ponderosa pine forest on an apparently uniform site, a second scale of pattern can be recognized: clumps or patches of trees similar in size and age, usually occupying $\frac{1}{10}$ acre or more (Fig. 1). The patchwork nature

FIG. 1. Typical stand of ponderosa pine in Arizona, showing distinct groups of trees of uniform age.

of the ponderosa pine forest is quite obvious—in fact, modern silviculture is based on it. Hallin's (1954) description of Unit Area Control emphasized that adjacent small stand units usually differ in age and structure and may require different cutting treatments. This idea is implicit throughout Pearson's (1950) monograph on ponderosa pine management. The origin and structural details of the individual groups have not been adequately considered, however.

The contiguous quadrat method proposed by Grieg-Smith (1952) was used to analyze the pattern of several typical old-growth ponderosa pine forest stands. This study has been reported more fully elsewhere (Cooper 1960). In brief, contiguous quadrat analysis requires counting the trees on each block in a grid of 256 or more small quadrat units. The quadrat units are combined for analysis into successively larger blocks and the variance is computed for each. If the vegetation is distinctly clumped, the variance of the blocks approximately equal in size to the mean clump area will be higher than that for the other block sizes.

Contiguous quadrat analysis showed that the trees comprising the mature forest stand are aggregated into distinct groups. The mean area of these groups ranges between .15 and .35 acre. Tree reproduction, occupying the intervals between the mature groups, is aggregated into groups or clumps of about the same size. Extensive increment boring established that nearly all the trees in any one group are of the same age. The mosaic pattern is of course not perfect. There is considerable variation in the size of clumps, and the boundary between adjacent patches is often indistinct.

A third scale of pattern is evident within a single even-aged clump, where there is often a two-fold variation in stand density from one part to another. The variation in stocking within an even-aged group is evidently the result of chance differences in seed dispersal and seedling survival during early stand development. This scale of pattern was not studied in detail.

Spacing Pattern of Individual Trees

The fourth scale of pattern, that of the individual trees in an even-aged group, was analyzed in stands of several ages on the Fort Apache Reservation. The spatial structure of uniform stands was studied on circular plots containing 30 to 50 trees. Five of these plots were in a homogeneous stand of 80-yr-old trees near Cooley Mountain, between McNary and Whiteriver, Arizona. Nine younger stands were sampled at Bog Creek, 10 miles east of McNary. The trees at Bog Creek were from 26 to 49 yrs old; stand density on the sample plots varied from 1300 to 8500 trees per acre. Stand density at Cooley Mountain was much less: 130 to 330 trees per acre. The trees on the Bog Creek plots had evidently never been exposed to fire; the Cooley Mountain stands had experienced several light surface fires early in their history.

On each plot, diameter at breast height of every tree was measured to the nearest $\frac{1}{10}$ in. The distance from the center of each tree to that of the nearest neighboring tree was measured to the nearest $\frac{1}{10}$ ft. The dbh of the nearest neighbor was likewise recorded. On 10 of the plots, distances and diameters of the second, third, and fourth neighbor were also recorded.

The mean of the distances from each tree in a stand to its nearest neighbor may be used to detect departures from randomness in the spacing pattern of individual trees. The mean distance between neighbors is at a maximum in a uniform hexagonal arrangement. It is zero at the other extreme, with all trees aggregated at a single point. The mean spacing distance in a randomly distributed stand lies between these limits. Clark and Evans (1954) have shown that the theoretical mean distance to nearest neighbor in a random stand may be readily computed for stands of known density. The ratio (R) of the observed mean distance between neighbors to that expected in a randomly distributed stand may be used as

an index of departure from randomness. If the trees are spaced more evenly than would be expected in a random distribution, R will be greater than one. A value of R smaller than one implies a clumped distribution.

Peilou (1959) has suggested that distances from random sampling points to the nearest plant are more satisfactory for detecting pattern in a plant community than are plant-to-plant distances. This is true only when the number of individuals per unit area is not accurately known. In this study, each sample plot was a separate entity, of known stand density.

A randomness index was calculated for each of 14 sampled stands (Table I). In all of the older

TABLE I. Randomness indexes, and correlation of individual tree diameters with distance to nearest neighbor and diameter of nearest neighbor

Stand Age (yrs.)	Trees per A.	Randomness Index (R)	Correlation Coefficients	
			Nearest Neighbor Distance	DBH of Nearest Neighbor
80	130	1.17	.34	
80	135	1.11	.28	
80	165	1.09	.46**	
80	225	1.12	.06	−.13
80	330	1.17*	.37**	
49	1300	.83	.21	−.25
49	3900	1.25	−.13	−.03
44	3500	1.06	−.16	−.05
44	8500	1.10	.35*	−.32
39	4500	1.08	.19	
39	5600	.92	.06	−.01
39	6500	.88	.30	.21
39	7700	1.07	.32*	−.07
26	2200	.81	.38	−.48*

** Significant at 1% level.
* Significant at 5% level.

stands, R was consistently greater than one, but in only two instances was the departure from randomness statistically significant according to the test suggested by Clark and Evans (1954). The fact that nearly all the calculated values of R were greater than one, however, almost certainly indicates a slight but real tendency toward uniform spacing.

On the assumption that the calculated values of R were actually valid, they were analyzed to see if stand age or stocking rate influenced the degree of non-randomness. A regression equation in the form

$$R = a + b_1 \log A + b_2 \log d \qquad (1)$$

was fitted to the several observed values of R, where A is stand age and d is stocking rate in trees per acre. For the 14 sampled plots,

$$R = 0.79 + 0.15 \log A \qquad (2)$$

The coefficient b_1 was significant at the 5% level; the coefficient b_2 was just short of statistical significance. This does not mean that stand density has no effect on stand randomness, but merely that the data do not conclusively show such an effect.

Drawing conclusions from data of doubtful statistical significance is of course subject to criticism. The data seem to show, however, that the trees in very young stands are distributed more or less at random, as a result of the random dispersal of seeds. As the stand matures, there is a slight tendency toward a more uniform spacing as competition increases and unsuccessful competitors are removed from the stand. At no age is there a strongly clumped or aggregated distribution of individuals.

The expected mean distances to second, third, and more distant neighbors in a stand of known density have been derived by Thompson (1956). He suggested that changes in the randomness index calculated for these more distant neighbors may indicate a larger scale of pattern than that indicated by distance to nearest neighbor. A randomness index was calculated for the distances to the second, third, and fourth tree on 10 of the plots. In every case, the successive values of R in any one stand were virtually identical. There is no evidence of a scale of pattern involving 3 or 4 trees in a group.

Distance to Nearest Neighbor

In even-aged stands, the mean tree size is determined by age of stand and by stocking rate. The more trees per acre in a stand of given age, the smaller they are on the average. The relation of tree size to stand density has been explored more fully elsewhere (Cooper 1961). Regardless of average size, there is wide variation in the diameters of the individual trees comprising an even-aged stand. The factors that contribute to this diversity in size are not well understood.

The distance from a given tree to its nearest competitor might be expected to influence its growth rate and hence its size. The more isolated a particular tree, the greater the volume of soil its roots can exploit and the faster its growth should be.

To test the effect of spacing distance on growth of individual trees, the correlation between dbh and distance to nearest neighbor was computed separately for each stand, using the Spearman rank correlation test. A high positive correlation would indicate that large trees tend to be

spaced farther from their neighbors than do small ones.

Rank correlation methods have fallen into disfavor in recent years, yet as McDonald and Green (1960) have pointed out, they have distinct advantages in many instances when a simple correlation, rather than a regression equation, is required. For calculations involving up to about 40 pairs of observations, rank correlation is much faster than the standard product-moment method. McDonald and Green (1960) have shown a close agreement between a large number of rank correlation coefficients and the corresponding coefficients calculated by the more conventional method.

Rank correlation has a further advantage when the relationship between the two variables is curvilinear rather than a straight line. Calculation of a curvilinear regression or correlation is equivalent to stretching the scale of one or both variables, but the relative ranking of the observations is not altered by so doing. In rank correlation, the value of the correlation coefficient is not changed whether dbh or basal area, distance or the square of distance, is used as the basis for computation. Tree diameters and linear distances between trees may be used without the laborious transformations that would be required in fitting a satisfactory regression equation.

Coefficients of correlation between dbh of each tree and distance to its nearest neighbor were computed for each of 14 stands (Table I). Two of the 14 coefficients were significant at the 1% level, 2 were significant at the 5% level, and the remainder were not significant. Two were in fact negative. There was no consistent relationship between degree of correlation and age or stand density, although there was a slightly greater correlation between tree diameter and spacing distance in the 80-yr-old stands than on the younger plots.

In any case, even the largest positive correlation coefficient of .46 found in one of the 80-yr-old stands means that distance to nearest neighbor accounts for only about 21% (r^2) of the observed variance among individual tree diameters. On the other plots, distance to nearest neighbor accounts for 12% or less of the observed variation in tree diameter.

For the 10 plots where distances to more distant neighbors had been measured, additional correlations between tree diameter and distance to second, third, and fourth neighbor, and various sums of distances, were computed. None of these combinations materially improved the correlation over that with distance to nearest neighbor. The most logical correlation would perhaps be that between tree diameter and the sum of the distances to the 4 nearest trees. In a few cases this correlation was higher than that with the nearest neighbor alone; in others it was poorer. No consistent trend was evident.

The lack of correlation between diameter and spacing was not due to lack of significant competition among trees. In each group of stands of similar age, mean basal area per tree was inversely related to stand density.

Pielou (1960) observed a highly significant correlation between tree size and distance to nearest neighbor in an all-aged ponderosa pine stand in British Columbia. She stated that this showed conclusively that the pines in the population investigated were competing with each other for available space. A positive correlation is almost inevitable between tree size and distance to nearest neighbor in an all-aged stand, where root systems of established trees rather effectively prevent the development of new ones within their zone of influence. The large number of observations insured the statistical significance of Pielou's correlation, but it is surprising that the coefficient is only 0.416. Even in this all-aged stand, distance to nearest neighbor accounts for only about 14% of the observed variance in tree size.

Relation to Size of Neighboring Tree

It seemed possible that rapid growth of a particular tree might to some degree inhibit the growth of nearby trees. Yoda *et al.* (1957) found that the weight of individual plants in several evenly spaced row crops was negatively correlated with the weight of the adjacent plant in the row, indicating a competitive interaction in which the larger plant tended to repress the growth of its smaller neighbor.

To test for a similar effect in even-aged ponderosa pine stands, rank correlation coefficients were computed for 10 of the plots, relating tree diameter to the diameter of the closest neighboring tree. All but one of these correlation coefficients were weakly negative, as would be expected, but only one was significant at the 5% level (Table I). Correlation with diameter of the nearest competitor accounts for an even smaller fraction of the total variance in size of individual trees on a plot than does distance to that competitor. No trend was recognizable relating degree of correlation to age or stand density. The stands showing the highest correlation in this analysis were not necessarily those that ranked high in the preceding section.

The correlations between tree diameter and the

summed diameters of the 4 nearest competing trees so obviously tended toward zero that they are meaningless.

Competition and Size Differentiation

Where competition is chiefly for light, those trees that are for some reason able to grow larger and taller than their neighbors quickly overtop their rivals. The losers in the contest for light are suppressed and retarded in their growth. Despite the intolerance of ponderosa pine to shade, competition for light in the open stands of the Southwest is rarely the governing factor in tree growth. Root competition for moisture and nutrients is usually more significant.

Under these conditions, the classic pattern of suppression does not occur. Each tree, large and small, grows at its own characteristic growth rate throughout its life. Large trees grow faster than small ones from the earliest stages; at least in young stands, there is no evident slowing of growth of small trees when they are finally suppressed (Cooper 1960).

If successful dominants in southwestern ponderosa pine stands actually suppress smaller trees by competitive consumption of growth requisites, a strong negative correlation would be expected between the size of a particular tree and that of its nearest neighbor. The lack of such a correlation is further evidence that the usual concept of suppression does not adequately explain differences in size of individual trees.

The fact that deviations from the mean in the spacing of competitors around a particular tree account for only a small fraction of the variability in tree size may appear to conflict with Staebler's (1956) observations in even-aged stands of Douglas fir (*Pseudotsuga menziesii*). He found that a thinning program which removed the chief competitor of a selected crop tree markedly increased the growth of that tree. Further but smaller increases in growth were obtained by removal of two or three competitors.

Staebler's experiments were carried out in established stands. Removal of nearby competitors in a closed stand created openings that the roots of the remaining crop trees could readily exploit. An increase in their growth would then be expected.

The ecological importance of the interconnection of roots among the several trees of a stand has been emphasized in several recent papers (e.g., Bormann and Graham 1959). There have been no extensive investigations of root grafting in ponderosa pine but it no doubt exists. The few studies of the rooting habits of this species (Woolsey 1911, Berndt and Gibbons 1958) fail to mention root grafts

Beskaravainyi (1956) found that in pine plantations 35 and 48 yrs old, about 50% of all trees entered into groups connected by root grafts. These groups usually consisted of 2 to 6 trees, occasionally as many as 11 or 12. The average diameter of the ungrafted trees was only about one-half that of the trees comprising the interconnected groups. There was more variation in size among the trees in groups than among isolated trees. The role of root grafts in ponderosa pine, and the extent to which root grafting alters competitive interactions among neighboring trees, is unknown.

Stand Development and the Origin of Pattern

In his fundamental paper on the nature of the plant community, Watt (1947) viewed an apparently stable forest community as a mosaic of patches differentiated by floristic composition and age of dominant. These patches continually change in relation to one another, as the trees comprising them reach maturity, die, and are replaced by a new set of young trees. Stages of this process go on throughout the forest, so that the climax vegetation is a vast patch-work of distinct phases dynamically related to one another. The various phases pass through any single patch like a wave in time, with all phases eventually represented on each small area. At any time the whole community in a stable environment shows a definite proportion of its constituent phases.

Patches originate when openings are produced by the death of a group of old trees or by a natural disaster. The openings fill with young trees, and a distinct patch is formed. The uniformity of seed distribution and the uneven occurrence of death of individuals should eventually smooth out these groups, so that after 2 or 3 rotations of the dominants, the vegetation should be distributed at random. Yet, the patches persist. Watt (1947) suggested that they impose their own habitat variations in time and space, and that because of these variations they tend to maintain themselves.

Such non-random patterns are apparently characteristic of most of the world's forest vegetation. An extensive survey of world literature on forest structure led Jones (1945) to conclude that a true all-aged forest, the ideal type of many foresters, is rare. Trees of every age class seldom occur in regular proportion on each unit area. He suggested that an even-aged mosaic structure is probably commoner than the available data indicate.

Richards (1952) found indications of a cyclical mosaic pattern in the tropical rain forest, but he observed that this pattern would be easier to detect in forests with fewer species and a simpler structure. Population fluctuations of all sorts tend to be larger and more easily observed in simple ecosystems than in complex. Population fluctuations and pattern development are particularly evident in the relatively simple ponderosa pine ecosystem.

The cyclical process of stand development in ponderosa pine forests has been discussed by Weaver (1943) and by Cooper (1960), especially with reference to the role of fire. The intolerance of ponderosa pine to shade, the infrequency of reproduction establishment, and the regular recurrence of natural fires all contribute to maintenance of pattern.

An even-aged stand of pine seedlings usually originates in a small forest opening, after a surface fire has prepared a suitable seedbed. Such an opening was once occupied by a group of mature pines, whose remains were consumed by a fire that exposed bare mineral soil. In the occasional years when a good seed crop and favorable moisture conditions coincide, a heavy crop of seedlings may become established in openings. Pattern development on a homogeneous small area begins with random seed dispersal and seedling germination.

Seedlings contribute little inflammable organic matter to the forest floor for several years, and surface fires that pass through surrounding stands ordinarily do not spread into very young seedling clumps until a quantity of litter has accumulated. As the young stand passes into the sapling stage, falling needles build up a mat of inflammable material that can support a light surface fire. Such a fire will ordinarily remove more small stems than large. The trees remaining after fire and other causes of mortality have taken effect maintain an essentially random spacing pattern, modified slightly in the direction of uniform spacing by a tendency toward selective mortality of very closely associated trees.

There is no evident tendency toward clumping of individuals at any stage in the development of an even-aged stand. Neither is there any important scale of pattern resulting from the morphology of the species, such as Kershaw (1959) found in Welsh grasslands. The closest approach to such a small scale morphological pattern arises from the fact that 2 trees obviously cannot be rooted at the same point. The relative lack of very close spacing seems, however, to be due more to competitive interaction among near neighbors than to physical interference.

A pattern of size differentiation, and of space occupancy by individual trees, develops simultaneously. The diameter distribution of trees in an even-aged stand follows a general log-normal form, and the shape of this distribution changes little as the stand matures (Cooper 1960). Distance to nearby competitors, or the relative size of those competitors, has only a slight effect on the ultimate pattern of tree size. In the absence of further data, most of the variation must be ascribed to genetic variability, or to undetected microsite differences.

If a later crop of seedlings should germinate beneath the canopy of an established stand, seedling growth is inhibited by shade. More important, the next surface fire, supported by debris from the overstory trees, will undoubtedly be hot enough to eliminate the seedling stand almost totally. Thus the even-aged nature of a mature group is maintained by fire. Eventually the stand reaches maturity, dies, and forms a new opening for repetition of the whole cycle. The typical ponderosa pine forest consists of a mosaic of such groups, each with its own characteristic internal pattern.

Patterns in space and time are easily observable in the ponderosa pine forests of northern Arizona. Similar patterns are no doubt characteristic of most vegetation types, but are more or less hidden in communities of greater complexity. To paraphrase Weiner (1948), plant communities are not stuff that abides, but patterns that perpetuate themselves.

Summary

Four types of pattern can be identified in the ponderosa pine forests of northern Arizona: (1) differences in density, growth, and species composition, the result of microenvironmental variation; (2) a mosaic pattern of even-aged groups, averaging about ⅕ acre in size and maintained largely by fire; (3) variations in stand density within a single even-aged group, primarily due to chance factors in early stand development; (4) the spacing pattern of individual trees in an even-aged stand.

Trees in young stands are randomly distributed, with a slight tendency toward a uniform distribution as the stands mature. No tendency toward clumping of individuals was detected. Average tree diameter in uniform stands is largely determined by stand density, but little of the variation in tree diameter within a single stand is accounted for by differences in spacing distance among the individual trees in the stand. Even less of the variation is accounted for by the differences in size of neighboring trees.

The clearly identifiable pattern in ponderosa pine forests is the result of the intolerance of the species to shade, the harsh environment which restricts the number of species present, and periodic natural fires that serve as the force that opposes the natural tendency of vegetation to take on a random distribution.

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A MICRO-LIMNOLOGICAL STUDY OF JAMAICAN BROMELIADS

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Introduction

My interest in undertaking this study was aroused by conversations with Dr. Archie Carr who has examined many tank bromeliads in various parts of Central America. His enthusiasm over the many types of life found in them, and his curiosity concerning how these organisms manage to live in such an environment, as well as the fact that very little was known about chemical and physical factors in the water caught in these plants, made the projection of such a study seem very worthwhile.

Fortunately, 2 other members of the Department of Biology, Drs. Howard T. Odum and James H. Gregg, were able to give me great technical assistance in developing micromethods for determining dissolved oxygen and dissolved carbon dioxide in the field. Drs. Carr, C. J. Goin and Mr. Erdman West who had recently been to Jamaica had observed that many large species of bromeliads grow very close to the ground and thus offer the investigator an excellent opportunity to examine them without spilling or disturbing their contents. Fortunately, Mr. George Cooley, who had supported some botanical exploration by Mr. West and a short exploratory trip by Dr. Carr, was favorably

impressed with the project and generously provided a grant to finance my 3 month study.

Dr. Bernard Lewis, Curator and Director of the Institute of Jamaica, Kingston, supplied most generous cooperation and members of the Institute's staff, particularly Mr. George Proctor, Botanist, helped both in advising me of good bromeliad sites and in identifying the species. Mr. Ron Bengrey gave cordially of his time and knowledge in facilitating the practical arrangements that a visitor must make on arriving in an unfamiliar country.

My study of bromeliad literature substantiated Dr. Carr's opinion regarding paucity of knowledge of the physical and chemical properties of the water entrapped by bromeliads. The monumental work of Picado (1913), other than reporting the associated fauna, was mainly concerned with chemical factors in relation to nutrition of the bromeliads. Material has been published on bromeliad-breeding mosquitoes acting as malarial vectors by Lutz (1903), Rozeboom and Laird (1942), Pittendrigh (1946, 1950a, 1950b) and many more. Pittendrigh (1948) made a study of the ecology of the plants. He (personal communication) found that virtually all the water he tested was acid, increasingly so, the greater the humus content. Picado attributed the lack of putrefaction in the water trapped by bromeliads to the absorption of the products of detrital decay by specialized scales on the leaves. Lutz (1903) remarked that the aquatic animals rarely come to the surface to respire but apply themselves to the submerged surface of the leaves to get oxygen (presumably formed by photosynthesis).

Methods

Considerable planning was necessary to decide what physical and chemical factors of the micro-aquatic environment of bromeliads could be tested in the field. It was obvious that the study would have to be made in areas remote from laboratory facilities and that equipment for analyses and collection of the biota would have to be carried to the plants on foot. A kit was constructed measuring only 6.5 × 14.5 × 4 inches, inside dimensions, which securely contained equipment for determining dissolved oxygen, dissolved carbon dioxide and for the colorimetric determination of pH.

Most of the material in this kit is standard, but the 3 pipettes calibrated to deliver .02 cc were constructed by Dr. Gregg. The ends of 10 cc syringes, to which steel needles are normally attached, were drawn out to a point and water samples and reagents were drawn into the syringes through these modified points. Heavy stopcock grease was employed to make the plungers of the syringes work very stiffly. This is important, since the mixing of the reagents for the micro-Winkler DO (dissolved oxygen) determinations must be done in the syringe preparatory to titration and, unless the plunger is very stiff, air will enter or some of the contents will be lost.

Dissolved Oxygen

The procedure of the unmodified micro-Winkler was as follows: (This is exactly like the Winkler method (Welch p. 207) except that I used one-fiftieth the amounts of all materials).

1. With the end of the nozzle held approximately ¼ inch below the surface, 5 cc of water was taken into the syringe.
2. With the aid of the 3 pipettes (each used only for one reagent) and with the small rubber hose attached to the end opposite their nozzles, .02 cc of manganous sulphate, .02 cc of KOH-KI solutions and .02 cc of concentrated H_2SO_4 were sucked into the pipettes and blown in that order on a small block of paraffin. The paraffin is used to keep these liquids in compact drops so that they may be sucked into the syringe without appreciable loss of material.
3. To insure complete mixing of each reagent in the syringe, air was drawn into the nozzle which was held in an upright position then expelled by gentle manipulation of the syringe plunger. Mixing was accomplished by a number of inversions of the syringe after each reagent had been added.[1]
4. Titration was performed in a small white crucible using standardized N/40 hypo solution and a pipette of 0.1 cc capacity graduated to 0.01 cc. Estimates to 0.001 cc were made visually. A burette holding 0.25 cc would have been better since I had to refill mine whenever the DO readings were above 4 ppm.

This method of DO determination was thoroughly tested by taking a rapidly repeated series of samples in my outdoor pool before leaving for Jamaica. Variations of less than 1% were observed in all cases.

[1] Fox and Wingfield (1938) state that dead space in the syringe nozzle may cause the unmixed KOH-KI solution to react with the H_2SO_4 liberating free iodine and causing DO determinations to be too high. They recommend the use of o-phosphoric acid instead of sulphuric to obviate this difficulty. Recently I compared results using each of these acids with the same equipment and procedure which I used in Jamaica in 1952. I boiled some distilled water and let it stand in a wide-mouthed jar for about 8 hours then performed my test which took about 75 minutes to complete. The results were as follows:

Using H_3PO_4		DO ppm	Using H_2SO_4		DO ppm
Hypo used	A.	6.56	Hypo	B.	6.60
to titrate	C.	6.64	used	D.	6.72

As the lowest reading was taken first and the highest last, as indicated by the sequence from A to D, the slight increase in DO may be attributed to the fact that O_2 was being absorbed by the water in the jar during the interval between the first and last tests. The small cross-sectional area of the nozzle and the second or so during which air is drawn into it should not allow any appreciable uptake of oxygen in the barrel of the syringe.

I felt some concern as to how long the hypo solution would remain standardized in Jamaica, and an extra supply was kept refrigerated. This refrigerated supply was used during the last 6 weeks of the study and, when compared to freshly standardized hypo on my return to Florida, it had changed less than 1%, or not more than the limit of accuracy of my apparatus.

Most of the water in bromeliads contains considerable amounts of organic detritus and it seemed possible that these, as well as nitrates, might seriously influence the DO determinations. A check on 2 samples from bromeliads, using the Rideal-Steward modification of the Winkler method, revealed too small a difference to be more than mechanical in nature. In one sample no DO was indicated by either method. Only straight Winkler analyses were made throughout the rest of the study with the realization that some errors may have resulted.

In one case where a very high DO value was obtained (8 ppm, Temp. 27°C, altitude about 3000 ft) it was found that this sample was 98% saturated as calculated from Rawson's nomogram in Welch (1948, p. 355). The dissolved CO_2 in the same sample was only 8 ppm. It was noticed, in sucking this sample into the syringe, that a number of small bubbles formed in the water as the pressure was reduced. It was also observed that the water contained a large concentration of unicellular algae. As the sample was taken at 11:30 AM from a plant in nearly full sun it is reasonable to expect that photoysnthesis would cause saturation of oxygen. This indirect evidence supports my belief that my micro-Winkler apparatus was giving reasonably accurate readings at the higher DO levels.

Free CO_2-micro-determinations

1. 5 cc samples of water from the bromeliads were sucked into a 10 cc syringe similar to that used for DO determinations, but the same syringe was never used for both DO and CO_2.
2. The sample was slowly ejected into a porcelain crucible used for no other purpose. The point of the syringe was kept against the bottom of the crucible.
3. A small drop of phenolpthalein indicator was added.
4. Titration with .02 N sodium hydroxide followed immediately using a 1 cc burette graduated to .01 cc. A solution of .002 NaOH was first tried in an effort to get greater accuracy but such a weak solution proved to be too easily affected by slight contamination.
5. CO_2 in ppm = number of cc of .02 N NaOH $\times$ 176.0.

pH determinations

Electronic pH meters were ruled out as impractical, both because of bulk and the fact that they would probably get out of adjustment because of rough treatment in the field. A Hellige colorimetric pocket comparator was used. Five cc water samples were taken. Bromocresol green-D, pH range 4.0-5.6, chlorophenol red-D, ph range 5.2-6.8, and phenol red-D, pH range 6.8-8.4 and corresponding disks were employed. Future studies on bromeliads using colorimetric pH kits should include in addition at least bromphenol-D, pH 3.0-4.6, or another dye to cover ranges well below 4.0, since I got a number of readings considerably below this although only one as high as 7.0

It was not until I had been in Jamaica for over a month that Dr. G. F. Asprey, at the time working at the University College of the West Indies, showed me apparatus of British manufacture, devised by Fox and Wingfield (1938), which Dr. Asprey assured me would have been satisfactory for micro determination of both oxygen and carbon dioxide. I regret that I did not have the opportunity of comparing the performance of this kit with mine.

Field Methods

On the first examination of bromeliads at the Hermitage Dam Area (Figure 1) it seemed that the maximum amount of data, with a reasonable expenditure of time, could be obtained by running my DO, CO_2 and pH test on the outermost leaf axil which appeared to contain enough water for the completion of these tests, and a like series of tests on the central reservoir. Of the 4 species of bromeliads examined at this station, *Guzmania monostachya, G. lingulata, Tillandsia excelsa* and *Hohenbergia* (*polycephala?*), only the latter contained enough water to make the DO and pH tests. No examination for the biota was made, since this was a trial to learn how to manipulate my apparatus in the field. No test for CO_2 was made at this time. These tests showed DO ranging from 1.5 ppm in the inner reservoir of *G. monostachya* to 3.4 ppm in the outer axil of *G. lingulata* and the pH ranging from 4.5 in the outer axil of *G. lingulata* to 4.0 in that of *Hohenbergia.* It was apparent that only the larger species of bromeliads would be likely to contain enough water to yield the desired data on dissolved CO_2, O_2 and pH. Acidity was surprisingly high.

Field studies were begun in earnest when I arrived at Chestervale, where many of the larger species of *Hohenbergia, Vriesia, Guzmania* and *Tillandsia* were often accessible, although some concern was felt concerning the amount of water that might be present because of the drought conditions at the time of my arrival (June 24, 1952).

The procedure adopted was to take first the pH in the outermost leaf axil that appeared to hold enough water for my tests and then to take that of the inner, or central, reservoir. The DO, dis-

FIG. 1. Map of Jamaica showing the Parishes bounded by dash lines. The principle collecting areas and other locations mentioned in the text are indicated by circular spots.

solved CO_2 and the temperature of the water were then determined in that sequence.

In the examination of the biota 2 methods were employed. Samples for microscopic examination were withdrawn from both the outer axil and from the inner reservoir, then put into 4 dram vials and corked. These were not filled more than halfway, since some air supply might be necessary to support life until a more thorough examination could be made. After carefully cutting the plant from its attachment, the larger animal forms were collected by gently breaking off the outer leaves, which either held no water or were judged to contain too little for my tests. When the water held by the outermost leaf tested chemically was reached, the still articulated portion of the plant was held upright over a 6" × 8" white enameled pan and the leaf removed, allowing what contents were left to flow into the pan. The plant, containing the central reservoir, still relatively undisturbed, was then propped in a nearly upright position while the organisms in the pan were collected. Some of the larger forms such as chironomous larvae and beetle larvae were handled with forceps and preserved in 70% alcohol or 10% formalin. Smaller forms such as mosquito larvae, copepods and ostracods were picked up in an eye dropper and preserved in separate vials.

Any other leaves intervening between the one just examined and the usual 3 to 4 leaves forming the central reservoir were removed and discarded. What now remained of the plant was held over a clean pan, which received the contents of the inner whorl. Some of the larger active forms such as beetles, frogs and certain orthopterans escaped, and no doubt some very small species were not detected. It is also probable that some forms which actually lived in the lower whorls, especially small helodid beetle larvae (*Cyphon* spp.), which are highly thigmotactic, hid on the plant axis and were not detected until washed out by water from the central reservoir.

Altogether, 20 bromeliads were examined in some detail in the Chestervale region (Fig. 1). Elevations varied from 5,000 to about 3,500 ft. At none of these places was the dissolved CO_2 taken because the .002 N, NaOH was found to be too weak to give reliable readings and the .02 N had not yet arrived. In some cases there was not enough water to complete both O_2 and pH test in both outer and central reservoirs. The pH data for this region are summarized in Table II.

RESULTS

It took me a considerable amount of time to appreciate some of the more important factors affecting the micro-environment within bromeliads. It was not until I had examined the 50th plant, a specimen of *Hohenbergia* sp. fully exposed to a strong wind for at least the previous 2 hours, and had obtained a fairly high DO reading of 5.8 ppm, that I realized the importance of exposure to wind. It was not until I had examined a species of *Hohenbergia* fully exposed to the sun and containing water supporting a very abundant growth of the green alga *Trachelomonas* sp., and had found a DO reading of 8 ppm, that I realized the importance of light in conjunction with associated algae. It then occurred to me that the time of day at which I made my determinations might make a tremendous difference in DO and CO_2 relationships. Finally, at plant number 70, I ran a day and night series on the same leaf axils. It was only then apparent to me that most of my previous DO and CO_2 determinations made only during the day, contributed but little to an understanding of the micro-limnology of these plants.

Because of the great amount of information

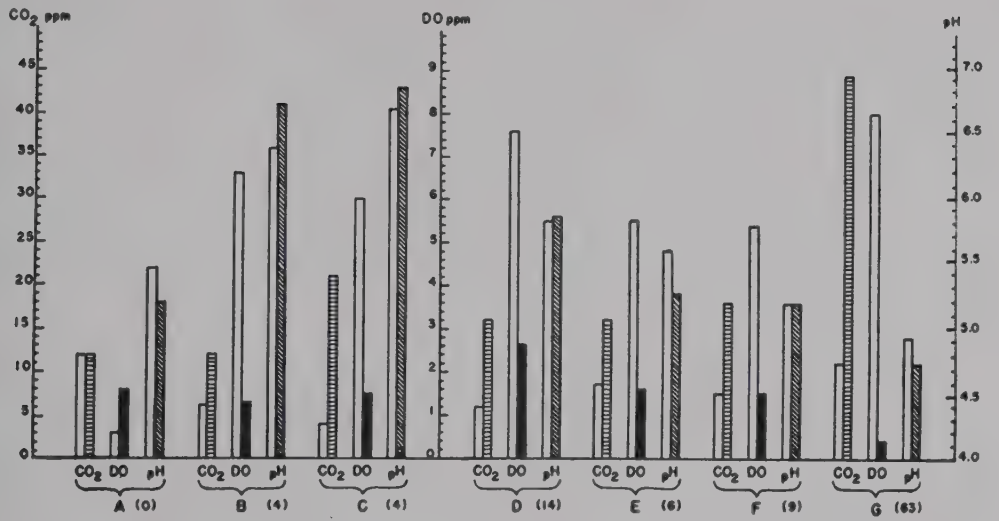

FIG. 3. Plant 70 nearly full insolation. The scales for CO_2, DO and pH are in sequence from left to right. The leaf axils examined are indicated by capital letters at the bottom, A being the outermost and G the innermost. For each axil there are 6 vertical columns, the white ones indicating by reference to the proper scale the daytime readings. The adjacent shaded or black columns indicate night readings for the same axis. The number of *Chironomus* sp. found in each axis is given in brackets at the bottom.

gained from the study of this plant it seems worthwhile to treat my findings in detail. A photograph of the plant prior to any examination of it is shown in Figure 2. The details of the chemical and physical data for each leaf axil examined are shown in Figure 3. A list of the associated biota in as much detail as I know it is given below.

FIG. 2. Plant 70, *Aechmea paniculigera* with the leaves lettered. "A" the outermost studied is hidden behind "D." East is to the left. Most of the lower unlettered leaves contained little or no water.

Plant number 70 was a large specimen of *Aechmea paniculigera* Griseb. It was growing in nearly full exposure to the sun on an outcrop of honeycomb limestone, at the top of the 3000 ft hill just south of the intersection of the Christiana and Spauldings roads. The 6 leaf axils studied were on the west side of the plant and thus did not receive much direct sunlight until afternoon. The central reservoir, G in Fig. 2, undoubtedly received direct sunlight much sooner. There were no fallen dead leaves from other plants covering the water in this plant. The weather was clear and no rain fell between the time of the day run (9:45 AM to 11:30 AM) and the start of the night run which began at 8:30 PM (about an hour after dark, August 29, 1952) and was completed at 10:30 PM. Starting with the outermost leaf axil that was judged to contain sufficient water for both day and night examinations (leaf axil A in Fig. 3) pH was tested first successively from A to G. The DO was then tested in the same order. Lastly the dissolved CO_2 tests were run. The removal of 20 cc of water from each leaf axil left at least 40 cc in each of them. In the night run, tests of each axil were made in the same order as above. The temperature of the water was taken in each leaf axil after all chemical tests were made. In the day series a trend toward higher temperatures was observed in moving from the outermost axils to the central reservoir: A = 24°C, G = 27°C. This was to be expected, since G received the greatest insolation. Night temperatures showed much less variation: A = 22°C, G = 21.7°C, with the intervening axils all falling between these readings. Since A was on the west side and should have received afternoon insolation the higher temperature there may be due to this factor but, as no

afternoon temperatures were determined, this is only speculation.

The morning following the completion of the chemical and physical tests a collection of the biota of each axil was made. The water was agitated by inserting a baster and sucking up and expelling the contents a few times. About 4 drams of this agitated water was put in labeled vials and examined under a compound microscope within a few hours after collection. The macroorganisms from each axil were collected in the manner already described.

The Biota of Plant 70

A. Macro-fauna: Numerous ostracods *Candonopsis anisitsi* Daday.
Micro-biota: Algae very few *Trachelomonas* sp., numerous gastrotricha, few ciliates and flagellates, bacteria abundant, copeopds frequent, 4 adult females of *Tropocyclops prasinus* cf. *mexicanus.*

B. Macro-fauna: *Chironomus* sp. 4, two species of ostracods, 3 of *C. anisitsi* collected and *Metacypris bromeliarium* (F. Muller) observed.
Micro-biota: Algae very abundant, mostly *Trachelomonas* sp., some *Micratinium* sp. ? and filamentous form, (*Mougeotia* sp. ?), ciliates few, flagellate, *Euglena spirogrya* few, copopods abundant both *Tropocyclops* and *Ectocyclops phaleratus,* rotifers (wormlike) abundant, gastrotricha observed.

C. Macro-fauna *Chironomus* sp. 4 larvae, 1 pupa; ostrocods, 4 collected of *M. bromeliarum* but *Candonopsis* also present.
Micro-biota: Algae not as abundant as in B, mostly *Trachelomonas* sp., bacteria fairly numerous, Copopods of both above species, 1 adult *Ectocyclops* collected, no rotifers nor gastrotricha observed.

D. Macro-fauna: *Chironomus* sp. 14; odonata, 2 small drangonfly nymphs *Erythrodiplax* sp., diptera, mosquito larva *Aedes inaequalis* (Grabham), 1 *Pentaneura* sp. and 1 *Cryptochironomous* sp. collected, ostracods 4 of *M. bromeliarum* collected.
Micro-biota: Algae very abundant, mostly *Trachelomonas* sp. and some *Micratinium* ?, ciliates common, worm-like rotifers common, *Euglena spirogyra* observed, no gastrotricha or copepods observed.

E. Macro-fauna: *Chironomus* sp. 6, odonata 1 nymph of *Erythrodiplax* sp., decapods *Metopaulias depressus* Rathbun, 1 small specimen; diptera 1 larva *Ae. inaequalis,* 1 *Cryptochironomous* sp., no ostracods observed, a single supraneuston hemipterid, *Microvelia laesslei* Drake and Hussey, no ostracods observed.
Micro-biota: Algae *Trachelomonas* sp. common, *Micratinium,* also present, copepods scarce, ciliates common, gastrotricha abundant.

F. Macro-fauna: *Chironomus* sp. 9, *Cryptochironomus* sp. 2, *Pentaneura* sp. 1, ostracods 3 specimens of *C. anisitsi* observed, hemipterids 1 specimen of *M. laesslei.*
Micro-biota: Algae abundant mostly *Trachelomonas* sp. some *Micratinium* ?, *Euglena spirogyra,* few rotifers and gastrotricha, some copepods *Troplocyclops.*

G. Macro-fauna: *Chironomus* sp. 63, one ostracod, *Metacypris bromeliarum, Cryptochironomus* sp. 1.
Micro-biota: Algae very abundant, mostly *Trachelomonas sp., Micratinium* ? few, bacteria fairly numerous, immature copepods numerous, only one adult male of *Troplocyclops* observed, no rotifers nor gastroricha observed.

Obviously no accurate quantitative data on the micro-biota were obtained. When I use the term abundant for the algae it means simply that the water appeared definitely green. The number of *Chironomus* collected is considered most significant because it is felt that all of these were counted and because of the large proportion of the biomass they represent, particularly in the central reservoir, G.

Relationships in Plant 70

The greatest fluctuation in DO occurred in the central reservoir G. There is roughly a reciprocal relationship between the DO and CO_2 in all axils except A in which very few algae were found. Obviously, oxygen formed by photosynthesis of the algae accounts for the 98% saturated DO reading in G. The same process would keep the CO_2 low during the day in spite of the respiration of 63 *Chironomus.* At night, even by 10:00 PM, almost all oxygen had been consumed, while the CO_2 had accumulated to approximately 45 ppm. In A, the higher night than day reading for DO seems best explained by its position on the west side of the plant, where direct light did not reach it until afternoon. As the DO readings were taken in the morning, little photosynthesis had taken place in this axil. However, by the time the night readings were made, more oxygen had accumulated and, because of the low biomass in this axil, consumption lagged. The intermediate degrees of fluctuation in the day and night DO and CO_2 readings in B to F seem explainable in the light of the biomasses involved, and from the presence of large numbers of algae and degrees of insolation. It seems unlikely that an appreciable amount of photosynthesis takes place in the submersed portion of bromeliad leaves as their bases are, at most, very pale green and often nearly white.

The relatively high pH readings in axils B and C were a puzzle until, in collecting the fauna, I noted that each contained fragments of a snail shell. The pH fluctuations in given reservoirs of this plant on the whole appear to be reflections of the amounts of CO_2 present. The water typically becomes more acid at night as the CO_2 rises. The exceptions, axils B and C, are thought to be due to the removal of 20 cc of the more acid surface water in taking the day readings, leaving only the more basic water nearest the calcareous snail shells. No explanation is apparent for the pH difference recorded at axil E.

In taking into consideration the fact that the night readings were started shortly after dark and

finished 2 hours later, it seems reasonable that, by projecting the night trend to dawn, the DO readings would have been much lower, particularly in axils B to F, as they all contained considerable amounts of green algae as well as a fair quantity of aquatic fauna. Likewise, higher CO_2 readings would be expected as the night progressed. It may also be inferred that DO readings would increase above those recorded in most of the intermediate axils if these determinations had been made later in the day, and also that the CO_2 would have been lower.

The most obvious correlations between the physical and biotic factors are those involving the number of algae and quantity of *Chironomus;* the central reservoir, G, had by far the highest concentrations of both while the outermost axil, A, had no *Chironomus* and the fewest algae. While G contained the most water this was not more than double that contained by any one of the axils examined. The *Chironomus* certainly fed directly on the algae, principally *Trachelomonas,* which were observed to clump together in immobile masses. The amount of detritus in this plant was very meager. The quantity of *Chironomus* did not appear to be directly proportional to the density of the algae. The presence of predatory forms such as the dragonfly immatures in axils D and E and the larvae of *Pentaneura* seem likely to be factors contributing to the smaller numbers of *Chironomus* observed in axils where algae were abundant.

The great abundance of *Chironomus* sp. in G, with only .4 ppm DO, is of interest in the light of the findings of Prossel *et al.* (1950) which show critical oxygen tensions for *Chironomus thummi* of 70 mm Hg and, for *C. plumosa,* 60 mm Hg at temperatures of 16-23°C. My reading of .4 ppm DO converts to a partial oxygen tension of only about 7.0 mm Hg at 22°C at an elevation of 3000 ft.[1] This is particularly interesting when one considers a statement of Leitch (1916) that the amount of oxygen that could be stored in the hemoglobin of *Chironomus* would last only about 12 minutes. So it would appear that the 63 *Chironomus* would have to endure on oxygen tension of 7 mm Hg, or even less, for at least 8 hours. Thus, it seems likely that these animals migrate up to the surface film when oxygen tensions get very low. Unfortunately, I did not observe the nocturnal behavior of the bromeliad fauna and this must be done before definite conclusions regarding DO requirements can be made.

While the high biomass of the central reservoir G is to be expected from the intense insolation extremly high algal content, the problem of sufficient concentration of nutritive salts to support the algae is raised. Inasmuch as the possibility of fallen leaves is almost ruled out because of the openness of the site, the possibility of excrement from birds and the chance falling in of other animal material, are suggested. The central reservoir, because it is the most open and is formed of 3 or 4 leaves, is most favorable situation to receive nutrients from such sources.

Study of Plant 75

I thought it desirable to test concepts formed in the study of plant 70 regarding the effect of insolation on biomass and on chemical and physical factors by studying bromeliads growing in shaded situations. One would expect that a picture similar to that observed in the outermost, most shaded axil A in plant 70, would obtain for all leaf axils and for the central reservoir of a plant growing in nearly full shade. This is shown to be substantially true from the study of a nearly completely shaded specimen of *Aechemea paniculigera,* growing on the same type of limestone as plant 70 at about the same elevation, just west of Knox College, Spauldings, Clarendon Parish.

In examining this plant 75, the night series was run first, otherwise the procedure was the same as for plant 70. Here the greatest variation between day and night readings was only .6 ppm in DO and a similar or greater degree of stability prevailed for the other factors (Figure 4). The relatively high pH of 6.1 in axil B proved to be due to the presence of fragments of a snail shell. The maximum temperature variation observed was only 1°C but, as the day readings were done early, more variation is indicated.

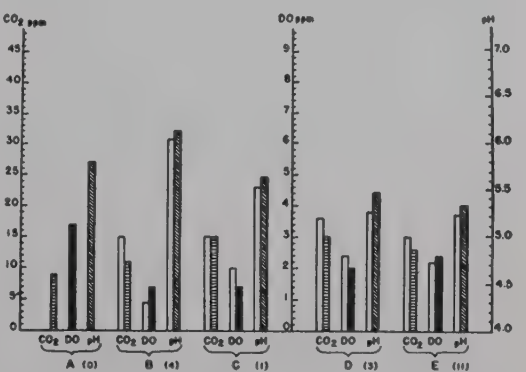

FIG. 4. Plant 75 in almost complete shade. This figure is to be read in the same manner as Figure 3. Leaf axil "A" gives only night readings as it had lost all water before determination could be made the next day. Fewer leaves are usually present in the less shade tolerant species when growing in heavily shaded places than when exposed to high insolation.

The biomass within the water cups was comparatively meager, a few ostracods, copepods and

a few ciliates. No algae were observed but bacteria were fairly numerous in C, D, and E. Eight young crabs, *Metopaulias,* were in B and one in D but, as indicated later, this animal appears to be largely, if not entirely, vegetarian. *Chironomus* sp. occurred in the following numbers: 4 in B, one in C, 3 in D, 11 in E. Two *Cryptochironomus* sp. were found in C and one in D. One larva of *Aedes inaequalis* was recorded but the axil in which it occurred is uncertain.

Environmental Conditions

The data from plants 70 and 75 suggest some generalizations regarding the relationships obtaining between the chemical and physical factors of the water entrapped in bromeliads and their aquatic biotas. Table I shows a generalized summary of these factors and the principal differences in energy sources and food chains.

Table I. Some of the more important relationships observed in bromeliads exposed to much insolation compared to those receiving little direct sunlight

	Plants exposed to much direct insolation	Plants heavily shaded by tree canopy
Producers	Inner reservoir-Mainly algae	Inner—Mainly dead leaves often having recently fallen.
	Outer leaf Axils-Algae few, small amounts of detritus, very little derived from decayed leaves.	Outer—Fairly abundant detritus from dead leaves in an advanced state of decay.
Principal Consumers	Inner reservoir-Large numbers of *Chironomus* spp.	Inner—Large numbers of *Cyphon* spp.
	Outer leaf axils-Few *Chironomus* spp.	Outer—Few *Cyphon* spp.
Temperature	Inner reservoir-Widest diurnal fluctuation	Inner—Moderate-little diurnal fluctuation
	Outer leaf axils-Wide diurnal fluctuation	Outer—Moderate-little diurnal fluctuation
DO/CO_2	Inner reservoir-Widest fluctuation DO high in day very low at night. CO_2 generally shows a reciprocal relationship.	Inner—DO low, often very low when fallen leaves are abundant, CO_2 high, often very high if fallen leaves are abundant.
	Outer leaf axils-Moderate fluctuation DO may be relatively high both day and night because of high surface/volume ratio and low biomass. CO_2 moderate.	Outer—DO moderate to fairly high and constant. CO_2 moderate and fairly constant.

Free surface volume relationships

Of all the large species of tank bromeliads examined, *Aechmea paniculigera* has the largest volume of water per leaf axil and the largest exposed surface/volume ratio. This is in part due to the more concave upper surface of the leaf at the level of the entrapped water, but it is mainly due to the great axial angle between the leaves forming the inner and outermost sides of the entrapped water (Figure 5). Most of the larger species of *Hohenbergia* are intermediate in these respects. The larger species *Vriesia* have the least concave leaves and the smallest axial angle.

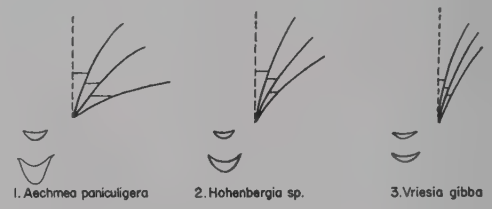

Fig. 5. A diagramatic illustration of the effect of growth habit on volume/surface ratios. The upper figures show variation in the axial angles of 3 of the larger genera. The shape of the water surface for the axes next to the central whorl and for the outermost whorl at water level is shown to the lower left of the larger figures.

The most important factor affecting the surface/volume ratio in any species is the age of the leaves. The younger leaves, being more nearly erect, entrap water to a greater depth than do the more widely spreading older ones. The exposed surface area becomes increasingly large as the older outer leaves assume a more nearly horizontal position. In the 3 genera discussed the axial angle of the oldest leaves still retaining water was greatest in *Aechmea* and least in *Vriesia.*

The surface/volume ratio is of obvious importance in affecting O_2 and CO_2 exchange between air and water. These exchanges are also better effected in windy situations by plants with widest axial angles.

When plants are growing in wooded situations the DO-CO_2 relationships are complicated by the fact that fallen leaves often completely cover the water surfaces inhibiting the exchange of gases; this results in high CO_2 and low DO readings. This phenomenon was nicely illustrated by plant 59, *Aechmea paniculigera,* growing on limestone 2 miles north of Sweetwater and exposed to about half sun. Here the central reservoir was so filled with dead leaves that no water was visible, while the outer axils, protected from falling leaves by the bromeliad leaves above, had their water surfaces exposed. My determinations for the central reservoir were, DO .5 ppm, CO_2 15 ppm, while an outer leaf axil showed a DO of 5.4 ppm and a CO_2 of 5.3 ppm.

The accumulation of dead leaves had these other effects: (a) the interception of light; in no case did I find an appreciable number of algae in cups so covered, (b) the large amount of detritus

formed from the decay of these leaves would tend to cause oxygen depletion and CO_2 accumulation.

Hydrogen ion concentration

There is apparently little if any correlation between the pH observed in bromeliads and the calcareous or non-calcareous nature of the soils. While it was observed that the highest average pH was obtained in the calcareous environs of Sweetwater and the lowest average pH occurred in the non-calcareous Chestervale area, there was no significant difference in the pH averages in the igneous Juan de Bolas region and the highly calcareous Christiana area (see Table II).

TABLE II. pH readings by regions

pH	Chestervale (non-calcareous) N=11	Juan de Bolas (igneous) N=8	Christiana (calcareous) N=6	Sweetwater (calcareous) N=7	Port Antonio (mixed) N=12
Outer axils					
mean.....	4.3	5.1	4.95	5.75	4.9
range.....	4-5.0	4.2-7.0	4-6	4.5-6.8	4.0-5.8
Central reservoirs					
mean.....	4.4	4.8	4.95	5.33	4.8
range.....	4-5.6	4-5.8	4-5.8	4.4-5.6	4-5.6

It seems reasonable to postulate that the fallen leaves would have higher calcium content in calcareous regions and it is possible that this may be a factor for the slightly higher average pH found in such areas. The only definite correlations with high pH and the contents of the water are those in which fragments of snail shells were observed. It is of interest to note that the lowest pH recorded, much below 4.0, was from a calcareous region, Christiana. There were, however, no dead leaves in this leaf axil.

In comparing different reservoirs either from the same or from different plants, there was no evidence that high CO_2 content was correlated with low pH. My highest CO_2 reading of 67 ppm was recorded in water with a pH of 5.4 while in another plant the reservoir showed a CO_2 content of only 14 ppm, yet had a pH considerably below 4.0. In some cases where dead leaves were abundant the water was the color of strong tea, suggesting the formation of humic acids. Yet, in an outstanding example of this, the pH was a not particularly acid 5.4. In other cases very acid readings considerably below pH 4.0 were obtained in reservoirs of unstained water with little associated organic debris.

Temperature

The lowest water temperature observed was 17.5°C. This was in plant 66, near Hardware Gap, elevation about 4,500 feet on August 23, 1952. This temperature was taken in the morning before direct sunlight had reached the plant. The highest temperature recorded, 30°C in plant 69, is discussed below. No night temperatures were taken at elevations above 3,000 feet where lower readings would be expected, nor were any taken near the hottest time of day in plants growing in full insolation near sea level. It is not likely that any of the lower summer readings would be critical to the bromeliad biota, but it seems very likely that the maximum temperatures within plants fully exposed to the sun at elevations near sea level would be critical for many forms (see discussion of plant 73).

A study of temperature variations in different leaf axils of plant 69, *Aechmea paniculigera*, growing on honeycomb limestone, elevation about 3,000 feet was made near Christiana, August 27, 1952. Leaf axil A was the outermost examined. B to F were progressively nearer the central reservoir G (Figure 6). The temperatures, taken when the plant was still shaded, were begun at 11:30 AM at axil A, thence progressively inwards with about a 3-minute gap between readings. Those on the right column were begun at 2:45 PM after the plant had been fully exposed to the sun for over 2 hours.

FIG. 6. Plant 69, *Aechmea paniculigera* with leaves cut at water level. Proof of the effective isolation of the water of each axil is shown by the fact that the level of water in each is progressively higher from outer to inner axils. The difference in level of water in the outer versus the innermost levels is about 6 inches.

An analysis of Table III shows, as one might expect, that the central reservoir G has the most fluctuation for the following reasons: 1) Being at the top of the "cone" it has more surface (not just free water surface) to lose or gain heat, 2) it receives more direct insolation, 3) it has the lowest free water surface/volume ratio, making the cooling effect of evaporation least. It seems probable that the intermediate axils have the more stable temperatures because they are shaded by the leaves

above and are insulated from heat exchanges by leaves and water, both above and below them. The lowest leaf axil, A, is exposed on its lower side to light and heat reflected from the limestone. The slightly higher morning reading of 23°C for A than for B and C is probably a reflection of this factor. On the other hand A's higher surface/volume ratio would tend to cool it more by evaporation. The above relationships would of course be influenced and complicated by such factors as elevation, relative humidity, wind velocity, the time and duration of direct sunlight and whether the plant is saxicolous or epiphytic. The external environment of this plant and the biota of its entrapped water was similar to that of plant 70. It is probable that temperatures above 30°C are critical to many of these forms but I am unable to cite any conclusive examples.

TABLE III. Temperature changes recorded from plant 69 before and after exposure to direct sunlight

Leaf axil	°C	
	Shade	Sun
A	23.0	26.7
B	22.7	27.6
C	22.7	28.0
D	22.5	29.0
E	22.5	29.3
F	23.0	29.5
G	23.0	30.0

I can give only one example where complete lack of macroscopic forms may have been due to excessive temperature. This was in a very large specimen of *Hohenbergia* sp., plant 73, growing on limestone, in full sun, only a few feet above sea level, about 6 miles SW of Lucea. Unfortunately, I do not have physical and chemical data on this plant, having only sampled it for fauna, but from its elevation, exposure to light, and the nature of its substrate, it seems likely that the water temperature within this plant may have reached 35°C. The only other factor likely to account for its sterility would be impermanence of its contained water, which would evaporate quickly and be transpired rapidly in such an environment. As the rainfall here is over 60 inches per year and as the plant contained an abundance of water, this factor seems unlikely, except possibly in late winter near the close of the "dry" season.

Volume of water present

While no actual measurements were made on the maximum volume of water contained in Jamaican bromeliads, a generous estimate for a large plant of *Aechmea paniculigera* (Fig. 6) can be reached by using the 7-inch new pencil for scale and figuring the volume of a truncated cone with a 7 inch base, a 2 inch diameter at the top and a height of 7 inches, giving a volume of about 4 liters. This volume includes detritus, leaf bases and the stem of the plant. Realizing that the mass is only approximately that of a truncated cone, it seems that a conservative estimate of the volume of water would be about 2 liters. This is far from the 20 liters reported by Picado (1913, p. 225) but is reasonable when compared to the 5 liters of free water reported in the gigantic specimens of *Glomeropitcairnia erectifolia* (Pittendrigh 1948). Some of the larger species of Hohenbergia in Jamaica contained comparable amounts of water (2 liters), probably enough to run a day and night series for most leaf axils (40 cc of detritus free water per axil). Even the larger Jamaican species of *Vriesia, Tillandsia* and *Guzmania* usually lack enough water for a single series of tests. In studying these species I was often forced to sample water from 3 different outer axils and 2 or more of the more centrally located ones, since the central reservoir often lacked enough water. It is therefore felt that my readings for these genera are not comparable to those obtained from *Aechmea* and *Hohenbergia.*

Another obvious factor affecting the amount of water present is precipitation. This factor was most critical in the early part of my study in the Chestervale area since very little rain fell during my 3 weeks there. Even in some large species of *Hohenbergia* the central reservoirs were only partially filled, containing only enough for a single series of tests (20 cc of detritus free water).

SOME OBSERVATIONS ON THE ECOLOGY OF JAMAICAN BROMELIADS

Pittendrigh (1948), gave 2 major ecological classifications for Trinidad bromeilads. Based on the methods by which the plants obtain moisture and nutrients, he recognized:

Type I Soil—Root
Type II Tank—Root (2 subdivisions)
Type III Tank—Absorbing trichones (4 subdivisions)
Type IV Atmosphere—(3 subdivisions).

Based on the degree of insolation, we recognized an exposure group, a sun group and a shade-tolerant group. Nearly all of the plants I examined fall into his classification III a, Tank-absorbing trichomes only, and into the sun group, but a few such as *Guzmania lingulata* fall into III c, the "Ephemeral" Tank, shade-tolerant group.

No large tank type bromeliads were found in the dry lowlands of the south central coast, but

in the southeast lowlands from about Port Morant eastward and the southwest lowlands from about Savanna la Mar westward some large *Hohenbergia* sp. were observed (Fig. 1). Apparently few tank bromeliads occur where the annual precipitation is under 60 inches. A moderate dry season of 4 to 5 months yearly with less than 4 inches of rain per month is tolerated. In a small lowland area along the north central coast east of Montego Bay no tank bromeliads were observed. This strip also falls below the 60 inch rainfall limit according to climatic data (Figure 7) given by Asprey and Robbins (1953).

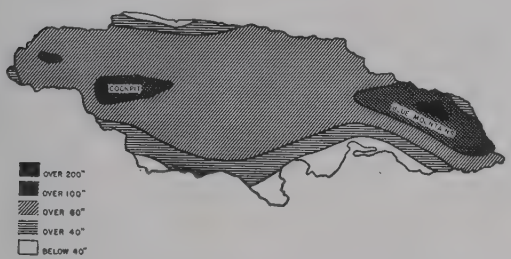

FIG. 7. Total average yearly rainfall compiled from 70-year records. A dry period occurs from January to March. Major wet periods are generally in May and October. (From Asprey and Robbins 1953.)

Strangely, the large tank types of *Hohenbergia, Aechmea* and *Vriesia* were rare or absent above 4,500 foot elevations, and on the extremely wet top of the John Crow Mountains, elevation about 3,000 feet, nothing but small tank species such as *Vriesia sintenisii* were found.

It seems likely that light may be limiting to the larger forms in the above areas and perhaps in the mist forests, where the sun rarely shines. According to Asprey and Robbins the upper ridges of the Blue Mountains are "enveloped daily in mist from 10-4, that is for a period of at least six hours." At the top of the John Crow Mountains direct sunlight is much rarer.

The comparative scarcity of large tank forms in the Chestervale region, even between 2,500-4,000 foot elevations, is due mainly to former clean clearing of the native forests and the lack of outcrops of substantial rock formations for the establishment of saxicolous forms. Nearly all the *Hohenbergias* found here were growing on mango trees which occur along the mountain trails. Other large tank forms as *Vriesia* spp. are found along stream courses, growing mainly on roseapple trees.

There is apparently a good correlation between habitat and the thickness and degree of cutinization of the tank bromeliad leaves. The numerous Jamaican Hohenbergias, with their thick and heavily cutinized leaves, are found in the sunniest most exposed situations even at the lowest altitudes where temperatures are highest. *Aechmea paniculigera,* with similar leaf characteristics, occupies similar situations but was not found near sea level. Large tank Vriesias were almost invariably found in more shaded places and at higher elevations (above 2,000 ft) than either of the above and have thinner leaves and less heavy cutinization. Smaller tank forms, with thin leaves and slight cutinization, such as *Guzmania lingulata* (shade tolerant, ephemeral tank), *G. monostachya, G. erythrolepis, G. capitoligera, Tillandsia complanata* and *Vriesia sintenisii,* are typically confined to more shaded situations or are found in the very humid mist forests. But occasionally they occur in exposed situations with extremely high precipitation about Millbank and in the John Crow Mountains.

Of the tank species with which I worked, many of the species of *Hohenbergia* and *Aechmea paniculigera* were observed to be both epiphytic and saxicolous in habit. Examples of the latter were largely confined to the honeycomb limestone outcrops of the Christiana and Sweetwater regions.

Relationships of the biota

As it was not discovered until late in this study that the physical and chemical qualities of the water in a leaf axil can vary tremendously in a single 24-hour period, little correlation with these factors can be deduced for the fauna from examinations made only in daytime. Minimal and maximal records for many of the environmental factors are given in Table IV. However, notes were made on such factors as exposure to wind, light, amount of dead leaves contained, elevation, and growth habit, and some discussion of these for the plants in which both day and night readings were obtained seems worthwhile.

Protozoa

In the evenings I examined samples of water collected from bromeliads studied during the day. Collections made in the mornings were kept in a shaded place with the corks of the vials removed. A compound microscope with a maximum magnification of 440× was used to study protozoa and other microscopic forms. I had very little success with identification using Kudo (1946), even though methyl cellulose was used to slow movement. However, many of the drawings of protozoa which I made were identified, at least to genus.

Protozoa were frequently encountered; the following were identified with a fair degree of certainty: *Colpoda* probably *cucullus, Colpidium campylum, Frontonia* sp. (*leucas?*), *Metopus* sp., *Chilomastix* sp., *Chilomonas paramecium, Aspidisca lynceus, Cyclogramma* (*Trichocystis*), *Asta-*

TABLE IV. Minimum and maximum readings recorded for DO, CO_2, pH and temperature for some of the aquatic fauna

Organism	DO range in ppm.	CO_2 range in ppm.	pH range	Temperature range °C	Number of tests
Geocentrophora metameroides	1.8———	———	4.0———	22.0———	1
G. applanata	2.2———	28.0———	5.8———	———	1
Gastrotrica	0.9——6.6	6.0—17.0	5.2—6.7	21.4—27.0	4
Nais-like oligochaeta	1.6——7.6	7.0—25.0	4.0—5.5	23.0—25.0	12
Tropocyclops prasinus	0.0——8.0	7.0—40.5	4.0—7.0	22.0—30.0	64
Ectocyclops phaleratus	0.5——6.6	5.3—67.0	4.3—6.6	21.0—29.5	11
Ostracods	0.0——8.0	5.0—40.0	4.0—7.0	17.5—30.0	66
Metapoulias depressus	0.48—7.6	6.0—67.0	4.0—7.0	21.0—28.0	29
Diceratobasis macrogaster	0.36—3.4	8.8—35.2	4.2—6.8	17.5—25.5	8
Erythodiplax sp.	1.0——7.6	14.0—19.0	4.0—5.6	21.4—30.0	7
Cyphon spp.	0.5——5.6	8.0—67.0	4.0—6.4	17.5—30.0	54
Telmatoscopus sp.	0.2——4.0	———	4.0—5.6	25.0—28.0	9
Aedes inaequalis	0.4——7.6	5.3—31.3	4.0—7.0	19.0—28.0	21
A. walkeri	0.025—4.0	12.0—41.0	4.0—5.8	21.0—28.0	21
A. stenei	1.0——5.0	7.0—28.0	4.5—5.6	———23.0	4
Chironomus sp.	0.02——8.0	4.0—46.0	4.0—6.8	22.0—30.0	40
Cryptochironomus sp.	0.02——8.0	5.3—46.0	4.0—6.6	17.5—29.5	32
Pentaneura sp.	0.02——8.0	6.0—46.0	4.0—5.8	18.5—30.0	34
Bezzia sp.	0.02——8.0	10.5—23.0	4.0—5.8	22.0—25.0	9
Eristalis sp.	0.8——2.5	———23	4.7—5.1	23.0—25.0	2
Hyla brunnea eggs and tadpoles	0.03——2.3	23.0—41.0	4.0—4.5	23.0—25.0	5

sia sp., *Vacuolaria virescens, Euglena spirogyra, Coleps (hirtus?), Bodo* sp. and *Petalomonas* sp. Dr. Bovee informed me that these ciliates are largely bacterial feeders with wide tolerance of physical factors. An actinozoan resembling *Clathrella* was observed at one station in the Chestervale area.

Turbellaria

Both *Geocentrophora metameroides* (Beauchamp) and *G. applanata* (Kennel) were collected at widely separated Jamaican localities. The former was recorded in Costa Rican bromeliads by Picado (1913). Dr. E. Ruffin Jones sectioned some of my specimens of this species and was unable to detect any mature male reproductive organs which, he informed me, have not yet been observed. One of my 3 records for Turbellaria is based on field observations only and the species is in doubt. While definite conclusions cannot be made at present on the oxygen requirements of these bromeliad inhabiting flatworms, it is noteworthy that in each case they were found only in the outer leaf axils, where the surface/volume ratio is highest, in plants that were shaded and at altitudes of 1,800 feet or higher. All of these factors would tend to keep the DO level from becoming very low. The recorded DO for the 3 stations were 1.8, 1.7, and 2.4 ppm, all readings taken in daylight. Dr. Jones informed me that, in his observations of *G. applanata* at Gainesville, they quickly die when kept in jars of water with low surface/volume ratios, but live well in flat containers with scarcely enough water to cover them.

Gastrotricha

These organisms were encountered only in clear water containing abundant algae in the Christiana region. Their tolerance of wide variations in the factors tested is shown in the detailed analysis of plant 70, Fig. 4, axils B, E, and F.

Oligochaeta

Nais-like forms which do not build tubes, similar to those recorded in bromeliads by Picado, were found in bromeliads growing in nearly full sun from just above sea level near Manchioneal to about 3,000 ft near Christiana. They were collected in all regions studied except the Blue Mountains. Inasmuch as they were found in plants exposed to both extremes of shade and sunlight and over such a wide range of elevations, these animals appear to be very tolerant of fluctuations in temperature, DO and CO_2.

Mr. W. R. Murchie examined some earthworm-like forms which occurred fairly frequently in detritus either covered by or saturated with water. Without sectioning the specimens, he thought that they might be of the genus *Diplocardia*. Picado recorded an earthworm-like form which appears to occupy the same niche in Costa Rican bromeliads. He observed the same blue-green iridescence in *Dichogaster picado* Michlsm. that I observed in *Diplocardia*.

It seems unlikely that oxygen could be a critical factor for these forms which are often 4 to 5 inches long and which readily move to the surface of the water-saturated detritus, or even from one axil to another.

Hydracarina

Most of the mites collected are considered terrestrial species. These were, however, collected in the water, no doubt having been dislodged from dead leaves that often covered the water cups of the bromeliads. Dr. Newell did mention that he found an aquatic mite of the genus *Arrenurus,* but he did not give my catalogue number so nothing of the aquatic situation can be given at this time. Most of the non-aquatic forms resemble those figured by Picado (1913).

Crustacea, Copepoda

Cyclopoid forms:

Picado recorded one copepod, *Cyclops phaleratus* Koch, in his bromeliad study; this is probably a synonym for *Ectocyclops phaleratus* which I collected from Morce's Gap, Sweetwater, Christiana and Juan de Bolas. In Jamaica *Tropocyclops prasinus* cf. *mexicanus* was much more abundant and widely distributed, being found in over 60 of the 80-odd plants examined. It does not seem worthwhile to record DO and CO_2 determinations as these forms spend much of their time against the surface film, while most of the water samples came from ¼ to ½ inch below the surface. However, for the record, the largest number of adults collected was 21 of *T. p.* cf. *mexicanus* from the central reservoir of an *Aechmea paniculigera* growing in nearly full shade, elevation about 3,000 feet, near Spauldings.

Harpacticoid forms:

Dr. Marjorie E. Carter very kindly separated all the harpacticoid copepods from the cyclopoid forms but as yet has only tentatively identified the harpacticoids as *Elaphoidella sewelli* s. str. These were collected from only 3 plants. One came from a *Guzmania monostachya* at Port Antonio which was shaded and had a pH of 5.6, but not enough water for further tests; another collection came from the same species near Millbank in which the water was not analyzed and the 3rd collection was from a *Hohenbergia* sp., well shaded from 2 miles east of Negril. Dr. Carter remarked that none of the plants from which I collected cyclopoid forms contained harpacticoids, which is unusual, as they are commonly found together.

Ostracoda

The essential data on this material have been published (Tressler 1956). It appears to be sufficient to quote from this paper as follows: ". . . ostracods were collected from water samples displaying a wide range of environmental conditions. Most species of ostracods are very tolerant of wide fluctuation in environmental factors and will exist under conditions of oxygen depletion, pollution and other unfavorable environmental conditions after other forms have perished. Some species are known to creep along the under surface of the surface film, apparently to secure oxygen."

In this paper Tressler described a new species *Metacypris laesslei* and mentioned that *Candonopsis anisitsi* had not previously been recorded from bromeliads. I observed what was undoubtedly the latter, in abundance with chironomous larvae, living in shallow water entrapped in pits on honeycomb limestone in the Sweetwater area. *Metacypris bromeliarum* was the 3rd species that I collected in Jamaica. *M. laesslei* may require lower temperatures than either of the other species as it was recorded only from elevations of 2,000 ft or more.

Decapoda

The bromeliad crab, *Metopaulias depressus* Rathbun, endemic to Jamaica, was observed commonly in the waters of the larger bromeliads at Juan de Bolas, about Christiana and in the Sweetwater environs. Dr. Fenner A. Chase, Jr. kindly supplied me with these additional recorded localities: Accompong, northern border of St. Elizabeth Parish; Mandeville, central portion and Newport, south central portion of Manchester Parish; Ewarton, northern portion of St. Katherine Parish; Hollymount, southern border of St. Ann Parish; Stony Hill, central St. Andrew Parish and hill back of Snug Harbor, St. James Parish. Rathbun (1918) stated that this crab "is found in the rugged limestone of Jamaica."

The known range of this crab is rather puzzling. All the records, except mine from Juan de Bolas, are limestone areas. All are at elevations above 1,000 ft, except possibly that of Snug Harbor, which I was unable to locate accurately. Why this crab has not been found in the limestone region in western Jamaica where elevations, large bromeliads and all apparent requirements are present, is not obvious. Nor is there any obvious explanation for their absence in the limestone region at the eastern end of the island, except that perhaps the high elevations of the Blue Mountains and the arid climate of the southeast coast act as barriers to dispersal. A possible barrier is a narrow connection, above the 1,000 ft elevation, between the most easterly station, Stony Hill, and the Blue Mountains. The factor of insufficient elevation seems most likely as there is similarly a very narrow connection above 1,000 ft with the unoccupied western part of the island (Figure 8). Certainly the lack of large bromeliads is not a factor.

The largest number of crabs collected from one bromeliad, *Aechmea paniculigera,* was 30: 3 adult males, 2 adult females and 25 young. Only .48

FIG. 8. Topographical regions of Jamaica. The Blue Mountain range in the east reaches a height of 7,402 ft. (From Asprey and Robbins 1953.)

ppm of DO was present in an outer leaf axil (pH 7.0) containing some of the young, but DO readings considerably higher were usually associated with the young crabs. There was no associated macrofauna in this plant, but crabs and *Cyphon* sp. larvae were frequently found together in other plants. It seems unlikely that DO is a critical factor for this species except perhaps in their early developmental stages, as they probably move freely above the water surface, needing only to keep their gills moist. Migration of the adult and juvenile crabs from bromeliad to bromeliad at night or during rainy weather seems likely, but the large number of nearly uniform sized young found at this station is indicative of little vagility in this stage.

In the examination of the stomach contents of adult crabs nothing except much macerated plant material was found. There was no evidence that the crabs feed on the bromeliads and they probably forage about at night, since none were observed out of the bromeliads during daylight.

No ovigerous individuals were observed among the 9 mature females collected. Microscopic examination of the water inhabited by adults revealed no larval forms. The smallest crabs found had a carapace about 3 mm wide. The key to the conditions limiting the distribution of this species may be in the factors affecting the early stages of its life history, and a planktonic diet for very young crabs seems likely.

I found *Metapaulias* only in the larger tank species, *Aechmea paniculigera, Hohenbergia* spp. and *Vriesia gibba,* but, inasmuch as these were the principal species examined in the range of the crab, it should not be inferred that these crabs are confined to the larger species.

Insecta

1. Odonata

Nymphs of a dragonfly and a damselfly were collected. The conditions under which the nymphs of an undescribed species of *Erythrodiplax* were found are given in the detailed analysis of plant 70. The largest number of damselfly nymphs collected in one water cup was 8 of *Diceratobasis macrogaster* (Selys). Associated fauna with both of these odonates were *Chironomus* sp., *Bezzia* sp. and *Cyphon* sp. It seems likely that *Chironomus* and *Cyphon* larvae are the principal prey of the bromeliad-inhabiting odonata in Jamaica, at least in their later instars. Calvert (1911) recorded *Mecistogaster* nymphs (a bromeliad inhabiting damselfly) as being cannibalistic. In this light it is strange that as many as 8 nymphs were found in one outer leaf axil. Calvert also recorded a mosquito larva and a copepod in the crop contents of a nymph.

Damselfly nymphs, many too young to be determinable, were taken from bromeliads at Hardware Gap, about Chestervale, at the east base of the John Crow Mountains, near Port Antonio and at Sweetwater. Dragonfly nymphs were taken near Christiana, Juan de Bolas, and Chestervale.

2. Hemiptera

A new species of *Microvelia* was collected and named *M. laesslei* by Drake and Hussey (1954). While this species appears to be strictly a supraneuston form, it does prey on the small aquatic organisms in the bromeliad water cups. Seventy-one specimens were collected from 14 bromeliads all growing at altitudes between 2,000 and 3,000 ft. The largest number of *M. laesslei* collected in one plant was 16. This species seemed about equally abundant in the larger types of bromeliads such as *Aechmea, Hohenbergia,* and *Vriesia* examined at Juan de Bolas, Christiana, and Sweetwater. This species plus *M. recens, M. ancona,* and *M. oaxacana* make 4 species of the genus known to inhabit bromeliads.

3. Coleoptera

a. Carabidae

Both adults and larvae of the genus *Colpodes* were found in water from bromeliads in the Blue Mountains and adjacent Portland Mountains. Adult specimens were determined by Darlington (1953) who, fortunately, was working on this group at the time of my investigation. Dr. van Emden, determined the larvae which he thought were probably of the same species as the adults associated with them. Picado (1913) reported *C. purpuratus* Reiche adults from Costa Rican bromeliads, but did not mention finding larvae.

The largest number of adults collected from one plant came from an undescribed, large, non-blooming bromeliad at Morce's Gap which yielded 19 *Colpodes punctus* Darl., even though some specimens escaped capture. No larvae were found. In another plant, also at Morce's Gap, a larva, possibly of *C. punctus,* was found associated with

an adult of this species. Darlington mentions that this species may be confined to high altitudes.

Colpodes bromeliarum Darl. adults were captured in 2 bromeliads, *Vriesia platynema* and *Tillandsia deppeana,* near Chestervale. *C. bruesi* Darl. adults were captured in *Hohenbergia* sp. at Hardware Gap; also captured in the same plant were 2 adults of *C. darlingtoni grandior* and one larva. Fortunately this plant contained enough water for a fairly complete analysis which showed: Temp. 19°C, pH 4.0, DO 1.1 ppm, CO_2 31 ppm. As the plant was growing in about half exposure to the sun, considerable variation in these figures is to be expected. These larvae may not be truly aquatic.

C. darlingtoni obtusior Darl. adults were collected in the largest number of plants, 7, all within a few miles of Chestervale and in the following species of bromeliads: *Hohenbergia* sp., *Guzmania capituligera, G. erythrolepis, G. lingulata, Vriesia platynema* and *Vriesia sintenisii.*

Of the 6 plants in which *Colpodes* larvae were captured, 5 had *Cyphon* sp. larvae associated with them, and as this was the macroscopic form most consistently associated with these predaceous *Colpodes* larvae, it may be the principal prey. It seems unlikely that the larvae of the bromeliad-inhabiting *Colpodes* are dependent on DO in the water of these plants since they probably move freely above the water and from leaf axil to leaf axil.

As I captured about 10 times as many adults of *Colpodes* as larvae, in spite of the fact that the adults are very active and many escaped me, it appears that I collected at a time when most had matured. No pupae were collected and (to my knowledge) this stage is undescribed. Many adults were observed in copulation, so larvae would probably be more frequent later in the year.

b. Dytiscidae and Hydrophilidae

Dr. Frank N. Young informed me that 2 species of adult aquatic beetles which I took from bromeliads near Sweetwater are a *Dytiscid, Desmopachria,* probably near *laevis* Sharp, and probably undescribed, and a *Hydrophilid* of the genus *Dactylosternum,* neither of which is probably confined to bromeliad water cups.

c. Helodidae

Larvae of the genus *Cyphon* were among the most abundant and most ubiquitous of the macroscopic forms encountered. They were found from near sea level to 5,000 ft in all major collecting areas, in practically ever bromeliad species examined which contained water. Dr. F. I. van Emden found at least 6 species represented and mentioned that his species 1, representing by far the largest number of specimens and collected at 38 of my stations, may actually represent a number of species, or at least several forms. Species 2 was collected at only one station, Morce's Gap, elevation about 5,000 ft, species 3, at only one station 10 miles south of Lucea, species 4, also at only one station, Sweetwater, elevation 2,000 ft, species 5, at 2 widely spaced stations, Juan de Bolas, 2,500 ft, and 10 miles south of Lucea, while species 6 was found at only one station, Hardware Gap, elevation about 4,500 feet. No pupae or adults were observed.

While these larvae are definitely aquatic, they crawl above the surface film and, because of their extremely hairy nature, carry a film of water with them. This habit no doubt enables them to obtain oxygen even when practically none exists in the bulk of bromeliad-entrapped waters.

These larvae were definitely more frequent when detritus, particularly dead leaves in various degrees of decay, was present. Picado (1913, p. 318) remarked on the similarity in appearance of nymphs (pupae) of *Scirtes championi,* which he reported so frequently in Costa Rican bromeliads, to the nymphs (pupae) of *Cyphon.* The larvae of *Cyphon* also bear a close resemblance to those of *Scirtes,* figured by Picado.

Cyphon larvae are almost certainly detritus feeders. Wintersteiner found *Cyphon* sp. larvae among dead leaves in a pond, W. E. Snow (unpublished data) found *Cyphon* larvae in tree holes in Illinois, and R. S. Usinger found larvae of the genus numerous in wet moss (the above 3 citations are from Leech and Chandler in Usinger 1956). *Cyphon* larvae along with *Chironomous* larvae apparently form the main macroscopic base-industry animals found in the Jamaican bromeliads.

4. Diptera

a. Tipulidae

An unidentified tipulid larva was collected from a *Vriesia sintenisii* at Comfort Castle, Portland Parish, in water with a DO of 2.0 ppm, and pH 5.6+. This specimen was damaged and not determinable to genus. Larvae which may be tipulids were collected from plants near Chestervale, Port Antonio, Sweetwater, and from about 2 miles south of Lucea.

b. Psychodidae

Both larvae and a pupa *Telmatoscopus* sp., probably *T. albapunctatus,* were taken from a *Vriesia sintenisii,* at Moretown, Portland Parish, and from 2 plants of *Guzmania monostachya,* and 5 plants of *Hohenbergia* spp., all near Port Antonio. The largest number of larvae collected in

one plant was 47. *Telmatoscopus* were also collected on the east side of the John Crow Mountains near Ecclestown. DO is obviously not a critical factor for these larvae. Why it is apparently confined to the northeast portion of the island is not known to me.

c. Culicidae

Larvae of *Aedes inaequalis* (Grabham) occurred frequently. In all, 22 plants contained these larvae, which were found in all of the major collecting areas.

Aedes walkeri (Theobald) larvae occurred in 23 plants but were found only at Juan de Bolas, Hermatage Dam and the Chestervale and Port Antonio regions.

Aedes stenei, recently described by Thomson (1956), was found in 3 plants at Juan de Bolas, one each near Sweetwater, near Ecclestown and 10 miles south of Lucea.

Only one collection was made of *Culex americanus* (Neueu-Lemaire), this was near Sweetwater and the following readings were obtained: pH 4.5, DO 2.0 and CO_2 18 ppm.

Three undetermined species of *Wyeomyia* were taken: species number 1 near Port Antonio and Union Hill, species number 2 at Hermitage Dam and Union Hill, species number 3 near Chestervale, Union Hill and Hardware Gap.

Dr. Knight remarked that the finding of 3 species of *Wyeomyia* and *Aedes inaequalis* in one plant, at Union Hill, is most peculiar. Inasmuch as I did not examine each axil of this plant separately, each species may have occurred in a different reservoir.

d. Tendipedidae

Chironomous sp. (strict sense) was found in all the major regions studied and in 21 plants. It was most abundant in the central reservoir of a plant of *Hohenbergia* sp. (56 specimens(and in the central reservoir of a plant of *Aechmea paniculigera* (63 individuals). Both of these plants were growing on honeycomb limestone, fully exposed to the sun, near Christiana. Both contained very large numbers of the green alga *Trachelomonas* sp. and gave readings of 8 ppm of DO in the daytime. *Cryptochironomus* sp., while also collected in all the major study areas and in 33 plants, was never taken in large numbers, 6 being the largest number taken from one plant. Larvae of *Pentaneura* sp. were also collected in all major collecting areas, but never more than a few in a single leaf axil, an expected finding in view of its carnivorous nature. These 3 genera were collected frequently and in water that varied so markedly in DO, CO_2, pH and temperature that these factors appear seldom if ever to be critical (see Table IV).

e. Ceratopogonidae

Larvae of *Bezzia* sp. were collected from only 11 plants in the major collecting areas about Port Antonio, Christiana and Sweetwater. The largest number of this carnivorous species was taken from the central reservoir of *Hohenbergia* sp., from near Union Hill, St. Mary's Parish. The prey of *Bezzia,* to my knowledge, is not known, but it may be significant that in 9 of 11 cases the larvae of *Cyphon* sp. were associated with it.

f. Stratiomyiidae

Soldier-fly larvae were found in 2 plants. A *Hohenbergia polystacha* at Chestervale contained too little water to be analyzed, except for pH, which was 4.2 in the central reservoir. Dr. Johannsen determined the larva to be of the genus *Nototelus.* The other specimen occurred in *Hohenbergia* sp., 10 miles south of Lucea. Dissolved oxygen and CO_2 are probably of little importance to these larvae which are adapted to respire above the surface.

g. Syrphidae

Rat-tailed maggots, probably of the genus *Eristalis,* were found in 3 widely scattered regions, in *Tillandsia deppaena* near Chestervale, *Aechmea paniculigera* near Millbank, Portland Parish, and *Tillandsia excelsa,* Hermitage Dam. The last was the only one of the above that had contents that were notably putrid. DO and CO_2 were probably of no consequence to these larvae which possess an extensible respiratory tube. It seems odd that only 3 of over 80 bromeliads examined in detail contained these larvae, as an abundance of detritus, their probable food, was present in most of the plants.

Vertebrata

The only vertebrates found in the bromeliads were adult and larval frogs. Fifteen of the 80 plants examined contained tadpoles of various sizes, all, according to Dr. Coleman J. Goin, *Hyla brunnea.* However, at Juan de Bolas, adults of the bromeliad breeding frog *H. wilderi* were collected in bromeliads. *Eleutherodactylus jamaicensis* adults were frequently captured in bromeliads but, according to Dr. Goin, do not breed in the water there. *H. brunnea* tadpoles were collected from large species of bromeliads in all of the major collecting areas. The maximum number of tadpoles collected from a single plant, *Tillandsia deppeana,* was 42. These varied in length from 12 to 37 mm, and averaged at least 25 mm. They came from a number of different leaf axils and from the

central reservoir. Associated with the tadpoles in this plant were earthworm-like oligochaetes, adult carabid beetles (*Colpodes bromeliarum*), mosquito larvae and ostracods. No protozoa were observed on microscopic examination. Several questions arise concerning these tadpoles. What do they eat? How do they get enough oxygen? In endeavoring to answer these questions a description of some of my observations and the ideas of others on this subject follow.

The tadpoles of *H. brunnea* usually occupied only the central reservoir and a clear, very viscous, jelly-like material filled most of the space leaving only about a quarter-inch layer of jelly-free water at the surface (Figure 9). This viscous material was observed by Panton and cited by Dunn (1926). Noble (1929) mentions that the "high viscosity is apparently due to the disintegration of the egg capsules." Noble states that it is hard to believe that the slimy liquid in the "nests" of Jamaican hylas would be saturated with oxygen. This jelly-like material seriously interfered with the pH, CO_2 and DO determinations, as it prevented the chemicals from mixing uniformly, but DO readings of less than .03 ppm were obtained on 2 occasions.

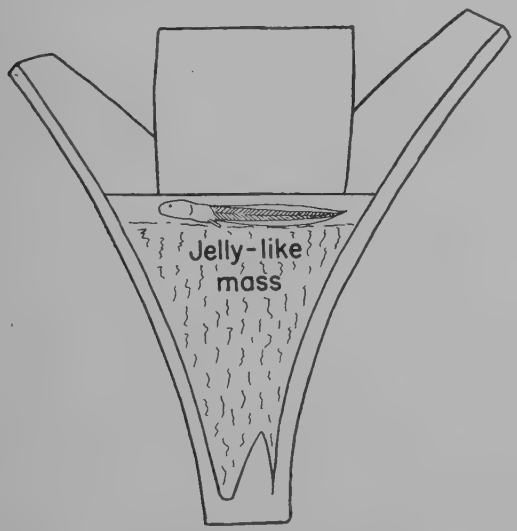

FIG. 9. A diagramatic axial section of the central reservoir of a bromeliad showing the relationship of jelly-free water occupied by a tadpole of *Hyla brunnea*.

I was able to observe the behavior of the tadpoles on a number of occasions. In each case they occupied the thin layer of jelly-free water at the surface, keeping their excessively long thin tails in constant agitation while not progressing appreciably. It appeared that their abdomens were stranded in the jelly and that most of the movement was imparted to the thin layer of water. In view of the low oxygen readings it seems that the function of the unusually long tail is to insure better aeration in the thin layer of water above the jelly. As Dunn (1926) observed a reduction of the branchial apparatus in the larvae of *H. brunnea,* it may be that the very long tail aids in cutaneous respiration. The question arises—would the extra oxygen consumed by this activity be more than compensated for by the higher oxygen absorption rate caused by the circulation of the water?

The question of what the tadpoles eat in such a closed system is stimulating. The quantity of algae that I observed associated with tadpoles was always meagre, but bacteria and ciliates were common in the jelly. It is perhaps significant that by the time the tadpoles approach metamorphosis the number observed in any single reservoir was only 6, or fewer, while much younger tadpoles, as many as 35 were observed in one reservoir. Cannibalism seems a possible explanation, but Noble (1929) failed to find any direct evidence to support this hypothesis.

My examination of many tadpoles showed that their intestines contained frog eggs, many of which were still enveloped by a jelly-like substance.[2] It is my belief that these eggs are of the same species as the tadpoles since, at all of my stations except at Juan de Bolas, *H. brunnea* was the only bromeliad-breeding frog observed. Dr. Goin informs me that in the Chestervale region, where the tadpoles were most abundant, *H. brunnea* is the only species known to breed in bromeliads. Dunn (1926) noticed the egg-eating habit of bromeliad-inhabiting tadpoles but did not mention that the eggs eaten were of the same species as the tadpoles. It is my opinion that the jelly-like mass, so generally associated with the tadpoles, is an accumulation of the jelly from many batches of eggs laid in the same water cup which already contained fairly well developed tadpoles. These, having eaten the eggs, leave behind most of their jelly-

[2] Taylor (1954) observed the undigested eggs of some arboreal frog, probably a different species from the tadpoles, in the much shortened, uncoiled upper intestines of the tadpoles, of *Anotheca coronata* collected in Costa Rica. My observations bear out that the uncoiled, shortened and thickened intestines in *H. brunnea* are often thick enough to accommodate 2 undigested frog eggs crosswise. Over 30 such undigested eggs were counted in one tadpole. Taylor does not give the maximum number of eggs that he observed in one tadpole but his illustrations indicate an even larger number than I found. Noble (1929) states that frog eggs were observed in the stomachs of tadpoles of *H. brunnea, H. wilderi, H. marianea* and *H. lichenata* and mentions that those found in the latter were larger and more pigmented than those devoured by the other species suggesting, but not proving, that tadpoles devour eggs of their own species.

like coverings. It may be that it is instinctive for gravid females to lay in water cups already occupied by tadpoles, thereby insuring that some of the larvae will obtain enough food to complete metamorphosis. It seems likely then that succeeding batches of eggs, not necessarily from the same female, serve the same function as milk in mammals, supporting the larvae until they are able to transform and forage for themselves.

The egg-eating of bromeliad-inhabiting tadpoles is probably characteristic. It seem unlikely that a newly-hatched larva could manage this with the much-reduced teeth of these species reported by Noble (1929). Microscopic examination of the jelly-like mass associated with *H. brunnea* tadpoles show it to be very rich in ciliated protozoa. Perhaps the very young larva are able to strain out enough of these by swallowing sufficient quantities of the jelly-like material containing protozoa, thus obtaining enough food to reach the egg-eating size.

Algae

Most of the algae were identified from drawings which I made from living material in Jamaica. However, algae were usually abundant only in bromeliads exposed to strong light in the Christiana region. Other than *Trachelomonas,* the most abundant and apparently the most important, the following were identified: *Mougeotia* sp., *Schroederia* sp., *Tribonema* sp., *Micratinium* sp., *Microspora* sp., the diatom *Pinnularia* sp., some other diatoms and at least one species of desmid.

Bacteria

Although bacteria were generally observed in the water of bromeliads and were often abundant, none were identified.

Summary and Conclusions

1. This study is an attempt to identify some of the apparently more important physical and chemical factors associated with the aquatic biota in the water cups of Jamaican bromeliads.

2. A compact field kit for testing pH, DO and CO_2 using 5 cc samples of water for each determination is described.

3. Only the larger species of bromeliads, *Hohenbergia* spp., *Aechmea paniculigera* and *Vriesia* spp., consistently contained enough water to perform all 3 tests.

4. It was found toward the end of the field study that plants exposed to strong light generally contain algae which form O_2 in the daylight and consume CO_2, giving near saturation readings of the former and low amounts of the latter. Night determinations of the same water cups show a nearly reciprocal relationship of these 2 dissolved gases, with DO readings of nearly .00 ppm.

5. Plants growing in nearly complete shade exhibit much more stable relationships of these dissolved gases.

6. Temperature fluctuations are also greater in the water of plants exposed to high insolation.

7. Plants growing in wooded situations accumulate large amounts of dead leaves, particularly in the central reservoir, effectively preventing the exchange of gases, thus resulting in very high CO_2 and very low oxygen readings.

8. The pH of the water cups is generally quite low, often considerably below 4.0. More basic readings are often correlated with the chance falling in of such calcareous material as fragments of snail shells. Only one reading as high as pH 7.0 was observed.

9. The surface/volume ratio of the water cups varied in different species of bromeliads, being generally higher in *Aechmea paniculigera,* intermediate in *Hohenbergia* spp. and lower in *Vriesia* spp., this being a function of the axial angle and the degree of concavity of the leaves. In a given plant, the oldest leaves still retaining water usually show higher surface/volume ratios and higher DO and lower CO_2, except where complicated by the presence of large amounts of algae, in which case the central reservoirs, if free from dead leaves, exhibit the higher DO and lower CO_2 readings during daylight.

10. The larger species of tank bromeliads occur generally from near sea level to about 4,500 ft elevation in regions of 60 inches of rainfall or more, except near the top of the John Crow Mountains, maximum elevation about 3,000 feet, where excessive rainfall and very little full insolation occur under almost constantly cloudy conditions. Only small, thinly cutinized species occur there.

11. The largest biomass is found in plants growing in full sun where algae form the base of the food chain. Plants growing in shaded situations usually support a lower biomass dependent on detritus, largely derived from decaying leaves, for their base-industry animals.

12. A varied aquatic biota was found, ranging through bacteria, algae, protozoa, gastrotrichs, rotifers, flatworms, oligochaetes, copepods, ostracods, fresh water crabs, numerous insect larvae of which helodid and carabid beetles, chironomids, *Bezzia,* mosquito larvae and odonate nymphs were frequent, as well as tadpoles of the tree frog *Hyla brunnea.*

13. Most of the biota is tolerant of wide ranges in chemical and physical conditions. Limited data indicate that the flatworms require fairly high oxygen tensions.

14. It is concluded that the tadpoles of *Hyla brunnea* subsist mainly on eggs of their own species.

15. Only one bromeliad was apparently sterile of macroscopic biota and, as this plant was near sea level and fully exposed to the sun, high temperature was probably the reason for its sterility.

16. The maximum volume of free water contained in a single bromeliad is estimated to be about 2 liters in large specimens of *Aechmea paniculigera* and *Hohenbergia* spp. The largest amount of water is usually in the central reservoir but even here more than 200 cc is exceptional.

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THE DISTRIBUTION OF SOME SMALL MAMMALS AND THEIR ASSOCIATED FLEAS FROM CENTRAL LABRADOR

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Jameson (1947), during a study of the fleas of the prairie vole (*Microtus* (= *Pedomys*) *ochrogaster* (Wagner)) and other associated small mammals in Kansas, found that some fleas were specific to their host while others were commonly present on 2 or more small mammals in the same habitat. In both these groups there were fleas that showed marked habitat preferences.

During the course of a trip to Labrador in 1956 the opportunity arose to investigate the occurrence of fleas on small mammals. A standard trapping technique was used, in 4 well defined habitats, to discover whether fleas exhibit habitat preferences as well as host preferences.

AREAS STUDIED

Knob Lake (Lat. 54° 48′ N., Long. 66° 48′ W) is situated in the middle of the Quebec-Labrador watershed. The forest types and the vegetation of the area, described by Hustich (1949), Hare (1950) and Rousseau (1952), represent a mosaic rather than a definite zone of transition from the taiga to the forest tundra. It is further complicated by water-dividing mountain ranges which rise to 2400-2800 ft for, on these exposed tops, the vegetation is similar to that of the northern Ungava tundra zone. There are intermediary conditions and the small mammals present in these zones therefore occur together within a small area.

In the Knob Lake area trapping for small mammals was carried out in 4 main habitats which approximate to certain of the categories of Hustich's (1949) classification.

(A) *Black spruce muskeg*

This forest type (Figure 1) is characteristic of the valley bottoms, or elsewhere, when drainage is poor and the soil tends to be consistently acid. It is included in the "wet series" of Hustich's classification.

Black spruce (*Picea mariana* (Mill.)) is the dominant tree species although both white spruce (*Picea glauca* (Moench)) and larch (*Larix laricina* (DuRoi)) occur occasionally. The ground cover is predominantly *Sphagnum* and there is often standing water. Labrador tea (*Ledum groenlandicum* Oeder) and leather leaf (*Chamaedaphe calyculata* (L.)) are important locally and spasmodically.

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FIG. 1. Muskeg.

(B) *Conifer-lichen woodland*

Hustich includes this type (Figure 2) in his "dry series" and again black spruce predominates, often assuming the "candelabrum" form. White spruce and larch intermix readily. There is a luxuriant carpet of caribou mosses *Cladonia* with odd patches of the feather moss *Pleurozium*.

(C) *Coniferous bush tundra or semi-tundra*

On higher and more exposed ground the lichen-woodland may give way to large areas which are covered by scattered low bushes (Figure 3), mainly of black spruce but in some places there is considerable admixture of alder (*Alnus*). The ground cover is predominantly *Cladonia*.

(D) *Tundra*

The highest ground supports only a ground layer when conditions are extreme (Figure 4). This is often luxurious with *Cladonia* and *Rha-*

FIG. 2. Lichen-woodland.

FIG. 3. Semi-tundra.

comitrium predominating but including *Salix* and *Vaccinium*. Some areas are devoid of vegetation and boulders, stones, coarse sands and gravels occur. It approximates to Polunin's (1948) description of hill summits and slopes in the southern part of Baffin island.

METHOD

The immediate vicinity of Knob Lake was trapped extensively and other areas, within a radius of 30 miles, were visited on a number of occasions. Trapping for small mammals took place from June 5 to July 28 1956.

FIG. 4. Tundra.

Museum break-back traps were used in areas representative of the 4 habitats. A standard technique was adopted and 100 traps were placed, without pre-baiting, 2 every meter, in a 50 meter transect across each selected area. They were baited with oatmeal and bacon fat and were left, normally, for 3 consecutive nights.

A new area was chosen at each of the subsequent trappings in a particular habitat because the number of captures in areas which had already been trapped was remarkably low even after 4 weeks had elapsed. Traps were in continual use in the muskeg, lichen-woodland and semi-tundra and the results are therefore based on a series of independent samples throughout the period of trapping in these 3 habitats. It was only possible to trap the tundra for one night and the results from this habitat are based on 100 traps.

An analysis of this, and other, trapping techniques will be published elsewhere, suffice it to record that no additional captures were taken, except in rare instances, after 2 nights trapping and the majority were taken on the first night. The results as a whole suggest that small mammal dispersion was slight.

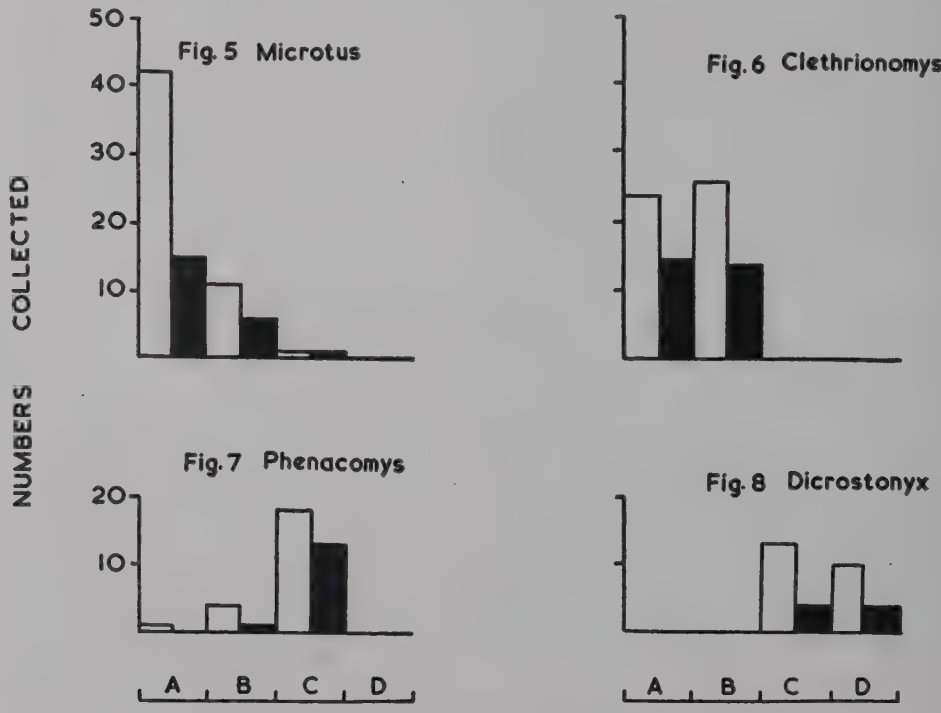
The traps were visited, normally, ever 6 hours and any captures were sealed in brown paper bags. Chloroform was used to kill any fleas present and a fine toothed comb was used to search the fur for additional specimens. The fleas were preserved in 70% alcohol with 5% glycerine added.

RESULTS

Small mammal captures totalled 152 from 3100 trap nights (a 4.9% return) and, of these, 74 carried one or more fleas (48.7%). The results are shown in Table I.

TABLE I. Shows the number and species of the fleas and small mammals collected

FLEAS				SMALL MAMMALS			
Species	No. collected	Average No. per mammal	Maximum No. on a single mammal	Species	No. trapped	No. carrying fleas	% carrying fleas
E. wenmanni	10	1.1	2	*Clethrionomys*	50	9	18.0
	2	—	—	*Microtus*	54	1	1.9
	2	—	—	*Phenacomys*	23	2	8.7
M. p. athabascae	13	1.9	5	*Clethrionomys*	50	7	14.0
M. asio	6	1.0	1	*Clethrionomys*	50	6	12.0
	29	1.9	4	*Microtus*	54	15	27.8
	1	—	—	*Phenacomys*	23	1	4.3
M. quirini	67	3.0	20	*Clethrionomys*	50	22	44.0
	13	2.2	7	*Dicrostonyx*	25	6	24.0
	18	1.3	3	*Microtus*	54	14	25.9
	67	4.8	14	*Phenacomys*	23	14	60.9



FIGS. 5-8. The total number of small mammals captured (white) and the number of small mammals carrying fleas of any species (black) is shown for 4 habitats (A) muskeg, (B) lichen-woodland, (C) semi-tundra and (D) tundra.

The distribution of small mammals

The following small mammals were captured:

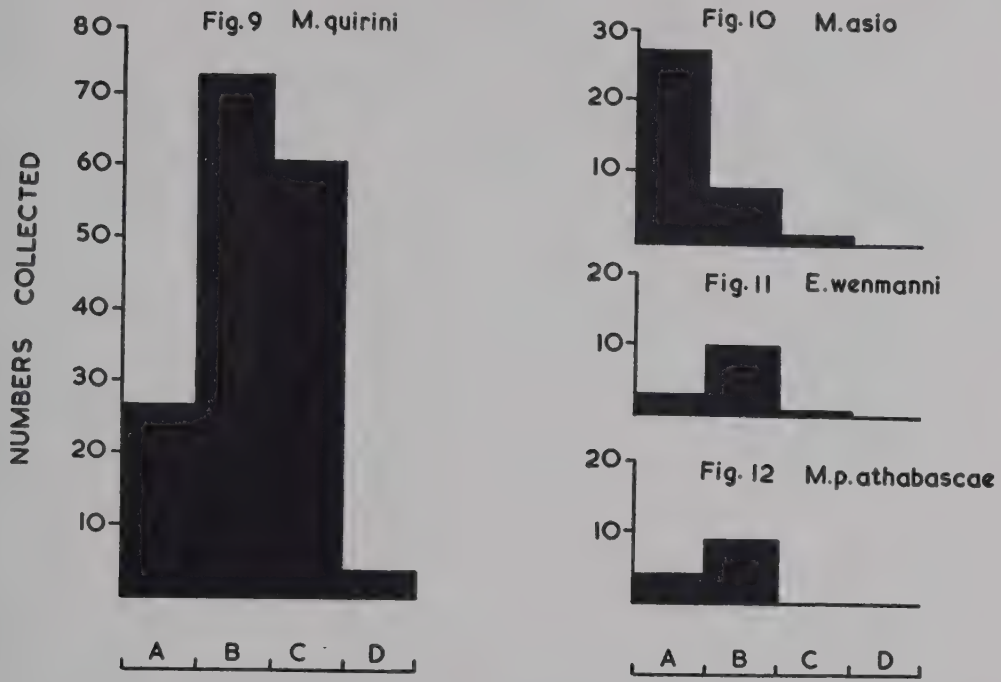
Clethrionomys gapperi ungava (Bailey)—*boreal* red back vole

Dicrostonyx hudsonius (Pallas)—Hudson Bay collared lemming

Microtus pennsylvanicus enixus Bangs.—meadow vole

Phenacomys ungava ungava Merriam

In addition, 3 *Sorex cinereus cinereus* Kerr and 3 *Zapus hudsonius ladas* Bangs. were collected. Three specimens of *Tamiasciurus hudsonicus ungavensis* Anderson were shot.



FIGS. 9-12. The total number of fleas collected from the habitats. (A) muskeg, (B) lichen-woodland, (C) semi-tundra and (D) tundra.

The relative density of the small mammals can be compared directly in the muskeg, lichen-woodland and semi-tundra as each habitat was trapped for 1000 trap nights. The tundra habitat was only trapped for 100 nights and thus multiplication by a factor of 10 is required to give approximate frequencies.

Figures 5-8 show the total numbers of small mammals caught in the 4 habitats studied.

Microtus was found in greatest numbers in the muskeg and was less numerous in the drier conditions prevailing in the lichen-woodland and semi-tundra (Fig. 5). *Clethrionomys* appeared in approximately the same numbers in the muskeg and lichen-woodland and was not trapped at all in the semi-tundra or tundra (Fig. 6). In the semi-tundra *Phenacomys* predominated although it was present in both lichen-woodland and muskeg (Fig. 7). *Dicrostonyx* was present in the semi-tundra but more numerous on the tundra (Fig. 8).

The 4 small mammals considered here did show clear and marked preferences for a particular habitat or habitats. *Microtus* certainly preferred the muskeg, *Phenacomys* and *Dicrostonyx* were characteristic of the semi-tundra and tundra respectively and *Clethrionomys* was clearly restricted to the lichen-woodland and muskeg.

The distribution of fleas

The following Siphonaptera were collected from small mammals trapped in the 4 habitats:

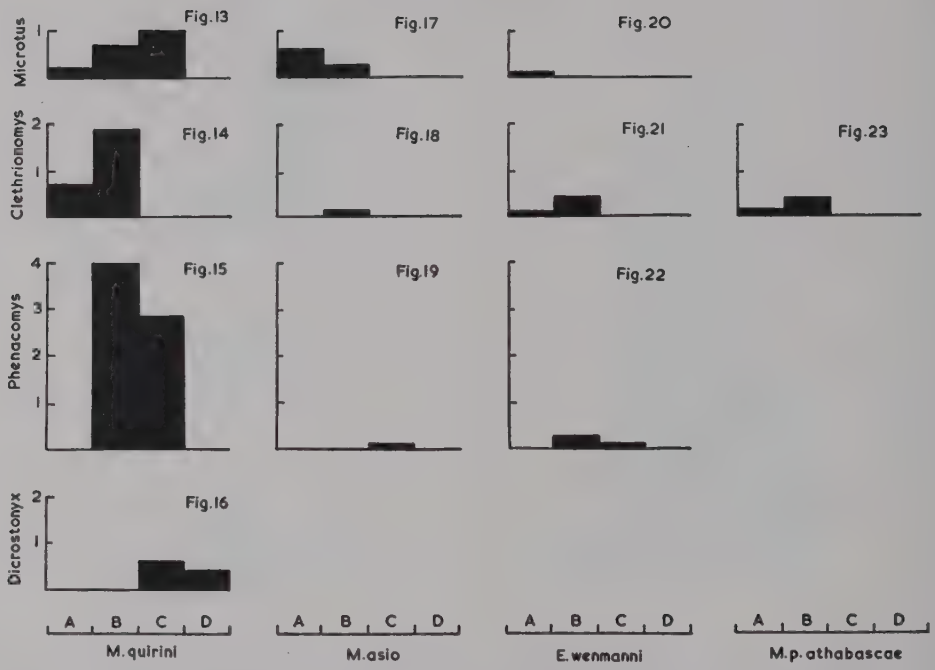
Epitedia wenmanni (Rothschild)
Malaraeus penicilliger athabascae Holland
Megabothris asio (Baker) (more typical of the eastern sub-species *M. a. asio* than the western *M. a. megacolpus*)
Megabothris quirini (Rothschild)

In addition possibly 2 female specimens of *Megabothris groenlandicus* (Wahlgren) were taken from *Dicrostonyx*. The absence of male specimens precludes a definite identification especially as in the trapping area this species may coexist with *M. quirini*.

Two specimens of *Corrodopsylla curvata* (Rothschild) were recorded from *Sorex* and one specimen of *Orchopeas caedens* (Jordan) from *Tamiasciurus;* the latter was, unexpectedly, more typical of *O. c. caedens* than *O. c. durus*.

Figs. 9-12 show the numbers of fleas recorded from the 4 habitats.

M. quirini (165 specimens) was, by far, the most abundant species and occurred in all 4 habitats. It was most numerous in the lichen-woodland but high numbers were recorded from the semi-tundra (Fig. 9). *M. asio* reached its highest frequency in the muskeg and appeared in suc-



FIGS. 13-23. The average number of fleas (calculated on the total captures of each small mammal species) carried by the small mammals in the 4 habitats (A) muskeg, (B) lichen-woodland, (C) semi-tundra and (D) tundra.

cessively lower numbers in the lichen-woodland and the semi-tundra (Fig. 10). Both *E. wenmanni* and *M. p. athabascae* were only collected occasionally and in view of their small numbers it is difficult to reach a conclusion in these cases although there was a tendency for both to be collected more frequently from the lichen-woodland (Figs. 11 and 12).

The interrelationships of small mammals and fleas

Table I shows, in the following cases, that 20-30% of the small mammals caried fleas; *Microtus* (27.8%) with *M. asio, Dicrostonyx* (24.0%) and *Microtus* (25.9%) carrying *M. quirini.* This percentage was even higher in the case of *Clethrionomys* (44.0%) and *Phenacomys* (60.9%) with *M. quirini.*

The maximum number of a single flea species carried by an individual small mammal was never very high except in the cases of *Clethrionomys* and *Phenacomys* where 20 and 14 *M. quirini* occurred respectively. The highest number of fleas, of 4 species, was 28 from a red back vole trapped in the lichen-woodland.

M. quirini was taken from all 4 habitats on a variety of small mammals. It was certainly the most catholic and most successful flea in terms of numbers despite the fact that it must be approaching the limit of its northern distribution (cf. Holland 1958). It achieved its highest numbers in the lichen-woodland and semi-tundra (Fig. 9) but was more abundant than any of the other species in the remaining 2 habitats except for *M. asio* in the muskeg (Fig. 10).

In the muskeg *M. quirini* preferred *Clethrionomys* to *Microtus* (Figs. 13 and 14) and in the lichen-woodland it preferred *Phenacomys* to *Clethrionomy* (Figs. 14 and 15) although its preferred host was least numerous in each case (*cf.* Figs. 5-7). Its association with *Phenacomys* is again exhibited in the semi-tundra (Figs. 15 and 16) although an alternative host, *Dicrostonyx,* was as numerous as *Phenacomys* in this habitat (Figs. 7 and 8). In the tundra it is recorded from *Dicrostonyx* (Fig. 16) at a frequency which is similar to that occurring on this species in the semi-tundra.

The preference of *M. quirini* for lichen-woodland and semi-tundra could possibly be explained in terms of the distribution of *Clethrionomys* and *Phenacomys.* On the other hand, it is recorded from *Microtus* and *Dicrostonyx* in the other 2 habitats and, in addition, a consideration of its

relative frequency on *Clethrionomys* in the muskeg and lichen-woodland (Fig. 14), where the small mammals were present in approximately equal numbers, suggests that this flea does in fact prefer the lichen-woodland. This is further substantiated by its distribution on *Microtus* where it occurs in higher numbers on animals trapped in lichen-woodland than in the muskeg (Fig. 13).

M. asio occurred most frequently in the muskeg where it has a clear preference for *Microtus* (Fig. 17). It is represented sporadically on *Clethrionomys* from muskeg and lichen-woodland and a single specimen was recorded from *Phenacomys* from the semi-tundra. In this case, apart from its ability to be represented at low frequencies on other hosts, the distribution of *M. asio* appears to be almost entirely accounted for by the distribution of its preferred host *Microtus*.

E. wenmanni occurred at relatively low density on all small mammals, except *Dicrostonyx*, throughout their respective ranges. It showed a preference for *Clethrionomys* (Fig. 21) in lichen-woodland but it was also present on *Phenacomys* and *Microtus* (Figs. 20 and 22). Its greater frequency on *Phenacomys* from lichen-woodland compared with semi-tundra suggests that this species, also, exhibits a preference for lichen-woodland.

It is known that *M. p. athabascae* is specific to *Clethrionomys* and thus it has only been recorded from the habitats in which this small mammal has been trapped (Fig. 23). *Clethrionomys*, however, was trapped in approximately equal numbers in the muskeg and lichen-woodland, and the higher numbers of this flea in the 2nd habitat suggests a preference for lichen-woodland.

Sex ratio

The number of fleas of each sex are shown in Table II. The departures from an assumed 1:1 ratio calculated on the totals from all habitats can be accounted for by chance alone for *M. asio* and *M. p. athabascae* ($P > 0.5$) but not for *M. quirini* or *E. wenmanni*. This disparity is reflected in the sex ratio of *M. quirini* on each of the small mammals except for *Microtus*.

TABLE II. The numbers of fleas of each sex collected from 4 small mammals. P. values are given for a chi-square test, on the totals, of the hypothesis of a 1:1 sex ratio

Host	*M. quirini*		*M. asio*		*E. wenmanni*		*M. p. athabascae*	
	♂	♀	♂	♀	♂	♀	♂	♀
Microtus	8	10	16	13	—	2	—	—
Clethrionomys	11	56	—	6	3	7	6	7
Phenacomys	10	57	—	1	—	2	—	—
Dicrostonyx	1	12	—	—	—	—	—	—
Totals	30	135	16	20	3	11	6	7
P value	<0.05 >0.02		>0.5		<0.1>0.05		>0.5	

Infestation

The number of infested and non-infested small mammals is shown in Table III. Males and females have an equal chance of carrying fleas ($P > 0.3$) except in the case of *Clethrionomys* where it is probable that males tended to be infested more frequently than females ($0.1 > P > 0.05$).

TABLE III. The numbers of small mammals infested and non-infested by any flea species. P values given for a chi-square test of a 2 × 2 contingency table

Host		Infested	Non-infested	Total	P value
Microtus	♂	15	18	33	>0.3
	♀	7	14	21	
Clethrionomys	♂	24	13	37	<0.1>0.05
	♀	5	8	13	
Phenacomys	♂	13	6	19	>0.8
	♀	2	2	4	
Dicrostonyx	♂	3	8	11	>0.9
	♀	5	9	14	

The mean number of fleas carried by sex is shown in Table IV. Of those animals that were infested the differences in the mean number carried by either males or females can be accounted for by chance alone ($P > 0.6$ in all cases).

TABLE IV. The mean and standard deviation is shown for numbers of fleas carried by the different sexes of 4 small mammals. P value given for a comparison of the means using a "t" distribution

Host		No. infested	No. of fleas	Mean & S.D.	P value
Microtus	♂	15	37	2.47±1.54	>0.7
	♀	7	12	1.71±1.25	
Clethrionomys	♂	24	82	3.42±5.52	>0.9
	♀	5	14	2.80±1.79	
Phenacomys	♂	13	56	4.31±3.80	>0.7
	♀	2	14	7.00±3.80	
Dicrostonyx	♂	3	4	1.33±0.45	>0.6
	♀	5	11	2.20±2.68	

The observed number of fleas carried (Table V), irrespective of species, only showed an agreement with a Poisson distribution in the case of *Dicrostonyx* ($P > 0.3$); for *Microtus, Clethrionomys* and *Phenacomys* the discrepancies are highly significant ($P < 0.01$ in all cases). A further analysis of the distribution of *M. quirini* on these 3 species and of *M. asio* on *Microtus* shows

TABLE V. The observed number of small mammals carrying 0, 1, 2, . . . fleas of any species. P values are given for a chi-square test of a fitted Poisson distribution

Host	NUMBER OF FLEAS					P value
	0	1	2	3	4 or more	
Microtus	44	8	9	3	4	<0.01
Clethrionomys .	22	12	7	4	6	<0.01
Phenacomys . . .	8	5	2	3	6	<0.01
Dicrostonyx . . .	18	10	1	1	—	>0.3

a marked and significant divergence from a Poisson distribution ($P < 0.01$).

When the numbers of species carried by the small mammals was considered (Table VI) this was found to approximate to a Poisson distribution in the case of *Microtus, Clethrionomys* and *Dicrostonyx* ($P > 0.3$) but not for *Phenacomys* ($P < 0.01$).

TABLE VI. The observed number of small mammals carrying 0, 1, 2, . . . species of flea. P values are given for a chi-square test of a fitted Poisson distribution

Host	NUMBER OF SPECIES					P value
	0	1	2	3	4	
Microtus	44	16	7	1	—	>0.5
Clethrionomys .	22	17	10	1	1	>0.3
Phenacomys . . .	8	14	2	—	—	<0.01
Dicrostonyx . . .	18	10	—	—	—	>0.3

DISCUSSION

The number of fleas taken from small mammal captures can only be used as a measure of relative density if those which are carried bear a constant, or interpretable, relation to those which are not. It has been standard practice to take the ectoparasite count as a basis for estimating the overall flea population despite the mounting evidence that many variables are involved. Some of these include seasonal differences (Evans & Freeman 1950), age and species of the mammal (Rumreich & Wynn 1945), type of habitat (Jameson 1947), time spent on and away from the host, climatic effects (Buxton 1938, Cole 1945) and the wide range of infestation.

In the present study a standardized technique has minimized some of these variables when considering the relative numbers of fleas present on small mammals, in 4 habitats, in a relatively small area. Traps were set in these habitats continually over an 8 week period and so seasonal effects, differences in age distribution of mammals in the population, and the gross effects of climate have been partially eliminated. Nevertheless the response of the different fleas to their hosts and the consequent wide range in infestation still remains an unknown factor.

The analysis of the distribution of the fleas on the small mammals suggests that the density of all the hosts was low and thus it might be suspected that fleas had difficulty in finding suitable hosts. The numbers of fleas taken from the small mammals was relatively low and only in occasional cases were large infestations recorded. Clearly the potential ability to carry a large number of fleas was rarely attained but this does not necessarily indicate that the overall flea population was low, as the percentage infestation approached 60% in some cases.

The analysis of the flea distribution on *Dicrostonyx* shows that both the numbers of fleas and the number of flea species can be accounted for on a random hypothesis. This suggests that only chance encounters take place between this species and other small mammals and that *Dicrostonyx* picks up fleas within its own range at random.

A subjective impression gained in the field suggests that when *Dicrostonyx* is trapped with *Phenacomys* in the semi-tundra the latter is most frequently caught in or near black spruce or alder bushes while the former is more characteristic of the intervening spaces. This supports the view that only chance encounters take place.

The numbers of fleas on *Microtus* and *Clethrionomys* show significant departures from a Poisson distribution and yet the number of species carried approximates to a random distribution. The numbers of encounters between these 2 species must be fairly high in view of the fact that they regularly share burrows, particularly in the muskeg, and probably utilize the same tracks and feeding sites. This would increase the chance of flea transfers and might account for the discrepancy from a Poisson distribution with respect to numbers.

As *M. quirini* shows a clear preference for *Phenacomys* it is likely that this explains the marked aggregation of the numbers of fleas on this species.

The random distribution of species on *Microtus* and *Clethrionomys,* as opposed to their aggregation on *Phenacomys,* can probably be explained in terms of the habitat preferences of the fleas. Apart from *M. asio* on *Microtus* in the muskeg the other fleas tend to prefer the lichen-woodland and semi-tundra and this cumulative effect is probably so large in the case of *Phenacomys* that it results in marked aggregation while it is of less importance in *Clethrionomys.*

The sex ratio of the fleas collected did not differ from a 1:1 expectation except in the case of *M. quirini* and possibly *E. wenmanni.* Cole (1945) has shown that the sexes of *Xenopsylla cheopis* exhibit different responses to temperature. More

males were present on the host at high temperatures and an approximate 1:1 ratio was achieved. At lower temperatures females predominated and this led to biased figures for the sex ratio. If a similar differential response occurs in *M. quirini* then the disproportionate sex ratio can be accounted for in terms of the low activity of males at temperatures which are close to minimal for this species as it approaches the limit of its northern distribution.

Finally, the present study supports and amplifies Jameson's (1947) work. It is clear in this case that the distribution of fleas cannot be totally explained in terms of the distribution of their hosts for 3 of the 4 species studied show definite habitat preferences. The reasons for these preferences are not clear. The wet conditions of the muskeg appear to be more suitable for *M. asio* than the drier conditions in the other habitats and the preferences of *M. p. athabascae, E. wenmanni* and *M. quirini* possibly reflect a compromise between the wet conditions of the muskeg and the rigorous conditions of the open tundra.

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Summary

The use of a standard trapping technique in 4 habitats in the Knob Lake area shows that 4 species of small mammals, *Microtus pennsylvanicus, Clethrionomys gapperi, Phenacomys ungava* and *Dicrostonyx hudsonius* exhibit habitat preferences ranging from muskeg, through lichen-woodland and semi-tundra, to tundra.

Both host and habitat preferences are shown by 4 species of flea, *Epitedia wenmanni, Malaraeus penicilliger athabascae, Megabothris asio* and *M. quirini.*

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COMPARATIVE ECOLOGY OF TWO BEETLES ESTABLISHED IN HAWAII: AN ANTHRIBID, *ARAECERUS LEVIPENNIS*, AND A BRUCHID, *MIMOSESTES SALLAEI*[1]

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INTRODUCTION

The 2 species of beetles used in this research are well suited for ecological comparisons. They occur together in areas generally undisturbed by human activity. The beetles are similar in that only one grub can develop in each seed of their leguminous hosts, but they differ with respect to their competitors and parasites. Finally, measurements of beetle density per pod can be made quite readily.

The anthribid, *Araecerus levipennis* Jordan, is an Oriental species which became established in Hawaii during 1954 (Ford and Chilson 1955). The principal host of *A. levipennis* in Hawaii is koa hole, *Leucaena glauca* (L.) Benth., but it can also develop in the seeds of 2 other legumes, native koa, *Acacia koa* Gray, and kolomona haole, *Cassia glauca* Lam. Both koa haole and kolomona haole are Neotropical in origin. *A. levipennis* has been the subject of a comprehensive investigation by Sherman and Tamashiro (1956).

The bruchid, *Mimosestes sallaei* (Sharp), is native to the Neotropical Region and the southern portions of the Nearctic Region. In 1918, it was found in Hawaii where its main hosts are 2 Neotropical legumes, klu, *Acacia farnesiana* (L.) Willd., and kiawe, *Prosopis chilensis* (Mol.) Stuntz (Bridwell 1919). Some observations on the bionomics and mortality of *M. sallaei* have been made by Cushman (1911), Bridwell (1920), and Hinckley (1960).

AREAS

Most of the research on beetle populations was conducted in 2 isolated areas on leeward (southern) Oahu. One area was on the tip of Waahila Hill, a ridge extending south-west from the Koolau Range. The other was on the outer southeastern slope of Diamond Head crater. Some collections were also made in areas at Maunalani Heights and Waialae Nui, 2 "ridge tips" similar to Waahila Hill.

During 1957, 1958, and 1959, the approximate annual temperature range in these areas was from 59°F to 90°F. Rainfall records for the same years showed that, on the average, about 3.2 inches fell from April through September and 19.3 inches from October through March at Diamond Head, while 13.3 and 26.3 inches fell during the same periods at Waahila Hill.

Koa haole was the most common legume in all 4 areas. At Diamond Head, however, klu and kiawe were almost as abundant as koa haole.

METHODS

Collections were of 2 types, the first in which samples of pods were taken weekly in one area as a crop developed and the 2nd in which regular collections of mature pods were made in all 4 areas.

The weekly collections of developing pods were designed to measure the oviposition and parasitization of *A. levipennis* and *M. sallaei* in koa haole and in klu. These weekly samples also yielded information on the susceptible periods of the hosts and the survival of the beetles. There were 2 series of weekly collections, at Waahila Hill during July and August 1958, and at Diamond Head during February and March 1960. In both series, approximately 100 green pods at a similar stage of development were marked on koa haole and on klu bushes. The total sampling area encompassing the plants with marked pods was about 25 square meters in each case.

Collections of mature pods were used to measure temporal and spatial variations in both infestation and mortality. The pods selected were those which had presumably been on the bushes throughout the previous 3 month period and had been brown for at least a month. Since the age of pods was sometimes difficult to determine, comparisons between areas have greater validity in this study than those between seasons. During the period from August 1958 through January 1960, collections of mature pods were made monthly at Waahila Hill and Diamond Head, and quarterly at Maunalani Heights and Waialae Nui. In each of the areas, samples were taken from those plants within a rectangle of approximately 1,000 square meters. Usually 50 to 100 koa haole pods were collected in each area but the size of the klu samples ranged from 25 to 50 pods. The smaller samples were usually taken during the drier months when fewer new pods were available. The

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koa haole pods were held for 2 months or more in dry containers. A 10 pod subsample was then dissected and counts made of undamaged seeds, seeds damaged by the combined action of *A. levipennis* and fungi, and seeds destroyed by *A. levipennis,* noting those in the latter category with grubs, pupae, adults, or adult exit holes. A 10 pod subsample of klu was dissected after a 5 or 6 week holding period. At that time, counts were made of those seeds with no external signs of damage, those damaged by *M. sallaei* or its competitors, and those with either bruchid or wasp exit holes. Also recorded for both klu and koa haole were the number of beetles and wasps reared from the entire samples.

Results

A. levipennis

As a preliminary to the collections of developing pods, the stage of maturity at which koa haole pods were first attacked was determined by tagging new clusters and making weekly observations. When the pods reached their full length and seeds began to enlarge, usually during the 5th or 6th week of pod development, *A. levipennis* started to oviposit. Prior to oviposition, the female chewed a hole at one end of a seed swelling. She then deposited a single white egg next to the seed. Finally, the hole was sealed with feces, a habit which apparently led to the growth of many microorganisms on the seed. Resinous exudation was also associated with oviposition.

In the weekly collections of developing koa haole pods, sampling was started as soon as oviposition sites were observed. Data on oviposition by *A. levipennis* in klu, as well as koa haole, are presented in Table I. There was no significant increase in oviposition after the pods turned brown. The period from first oviposition to first emergence in koa haole was 8 weeks at Waahila Hill and 5 weeks at Diamond Head. Survival of *A. levipennis in* klu was very low. Those few larvae which hatched from eggs in the fleshy klu pods usually drowned and rarely reached a seed. Survival of *A. levipennis* in koa haole is shown in Fig. 1.

Table I. Oviposition by *A. levipennis* (Oviposition sites per 10 pods)

Place and date	Koa Haole	Klu
Waahila Hill—1958		
Jul. 12	52	10
19	135	29
26	268 (Browning)	46
Aug. 2	307	61 (Browning)
9	232	46
16	284	85
23	282	78
30	241	63
Diamond Head—1960		
Feb. 9	32 (Browning)	35
16	49	42 (Browning)
23	37	36
Mar. 1	41	44
8	47	25
15	55	36
22	57	34
29	38	16

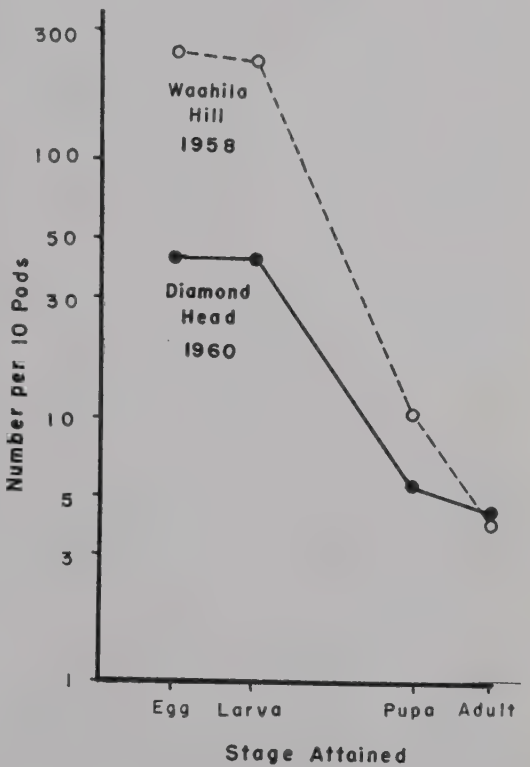

Fig. 1. Survival of *A. levipennis* in Koa Haole.

Egg mortality, although slightly greater at Waahila Hill, was relatively unimportant during both series. In the heavily attacked koa haole pods collected at Waahila Hill, larval mortality, especially during the first instar, was quite conspicuous. Larval mortality was also important at Diamond Head but occurred during the 2nd and 3rd instars.

The mite, *Pyemotes boylei* Krczal, was first observed at Waahila Hill in the 4th collection and killed half the pupae and adults in the 8th collections. Parasites were less common during the Diamond Head series. During the last 3 collec-

tions, however, a few specimens of the wasp, *Eupelmus cushmani* (Crawford), and the mite were observed.

In the collections of mature pods, the number of seeds damaged by grubs of *A. levipennis* was considered to be a useful index of infestation, although more than one larva may have been associated with a damaged seed and a single larva may sometimes have damaged several seeds. In Table II, the collection results are summarized. Oviposition sites were counted only during the last 9 months of the 18 month collection period.

TABLE II. Oviposition, infestation, and survival of *A. levipennis* in koa haole pods

Area	Oviposition sites/100 seeds	Total seeds	% infested seeds	% survival from infestation to emergence
Waahila Hill	119.1	3158	87.0	4.2
Diamond Head	81.9	3144	65.1	5.2
Maunalani Heights	94.3	1115	64.7	7.6
Waialae Nui	113.4	1178	77.9	5.6
		8595		
Season				
Summer (Jul.-Sep.)	103.0	2853	71.0	6.4
Autumn (Oct.-Dec.)	73.4	2893	66.5	5.7
Winter (Jan.-Mar.)	c. 144.1	1420	92.1	2.9
Spring (Apr.-Jun.)	129.9	1429	83.0	4.2
		8595		

From Table II, it would seem that survival of *A. levipennis* was lowest in infestations above 80%. However, no clear relationship between damage and survival was apparent when the infestations were lighter. During the latter half of the collection period, a total of 4415 oviposition sites were counted. Using this figure as a base, mortality from *Pyemotes* was 2.6% and parasitization by *Eupelmus* was less than 1%.

The results of collections indicated that, despite generally low parasitization, mortality of *A. levipennis* larvae was quite high. Therefore, further studies were made to determine the major sources of this mortality. The first of these special studies was designed to determine the survival of *A. levipennis* under wet and dry conditions. Two lots of 10 koa haole pods each were collected in Manoa Valley on July 3, 1959. They were placed in polyethylene bags, one with water, one without, and held in the laboratory until August 4, when dissections and counts were made. On the average, there were 20 oviposition sites and 16 seeds per pod. Those which had been kept damp yielded 3.5 adults per pod, a survival of 17.5%, but those held in dry bags produced none. These, and other experiments with less heavily infested pods, supported the conclusion that *A. levipennis* larvae cannot complete their development on dry koa haole seeds, although they may survive more than 6 months in the 3rd larval instar.

Mortality under wet conditions usually occurred early in larval development and could be attributed to the increased exudation and growth of fungi in damp pods. Only in a few cases did 2 grubs destroy large portions of the same seed, directly contributing to their own starvation.

M. sallaei

By tagging new clusters, it was determined that *M. sallaei* first oviposited on the basal end of green klu pods, sometimes as early as the 5th week of pod development. When the pods started turning brown, during the 10th to 12th week, oviposition usually increased. The attack continued for months, oviposition occurring even on year-old pods in which all the seeds had been destroyed. Although the eggs could be laid anywhere on the surface of the pod, certain points, next to ridges or inside wounds, seemed to be favored.

In the collections of developing pods, the period from the first oviposition to the first adult emergence was 7 weeks at Waahila Hill and about 5 weeks at Diamond Head. Oviposition data for *A. levipennis* on klu have already been summarized in Table I. It was usually more difficult to determine the number of eggs laid by *M. sallaei* on klu. The eggs were often destroyed, presumably by ants, although recovery of eggs was fairly good in the first 4 collections of developing klu pods at Diamond Head. In order to estimate egg mortality at Waahila Hill, it was necessary to use exposure techniques. Females of *M. sallaei* were allowed to oviposit on brown pods in the laboratory, and the pods were then fastened to klu bushes at Waahila Hill. The results from the Waahila Hill exposures and the Diamond Head collections are shown in Table III.

TABLE III. Mortality of *M. sallaei* eggs

	Waahila Hill (Exposures)		Diamond Head (Collections)	
	Number	%	Number	%
Pods	23	—	80	—
Eggs	98	—	470	—
a. Removed by ants	39	39.8	?	—
b. Parasitized by *Uscana*	5	5.1	51	10.8
c. Addled	47	48.0	326	69.4
d. Hatched	7	7.1	93	19.7

Although there were only 93 hatched eggs in the Diamond Head collections, 126 larvae, pupae, and adults of *M. sallaei* were recovered. This

would suggest that the total number of eggs laid on the klu pods collected at Diamond Head was at least 503. In the series at Waahila Hill, 23 larvae, pupae, and adults were recovered even though no hatched eggs were observed. Assuming that the exposures gave a representative picture of egg survival at Waahila Hill, a minimal starting population of 324 eggs can be postulated. Using these figures, rough survivorship curves can be constructed for *M. sallaei* at Waahila Hill and at Diamond Head. These curves are shown in Figure 2.

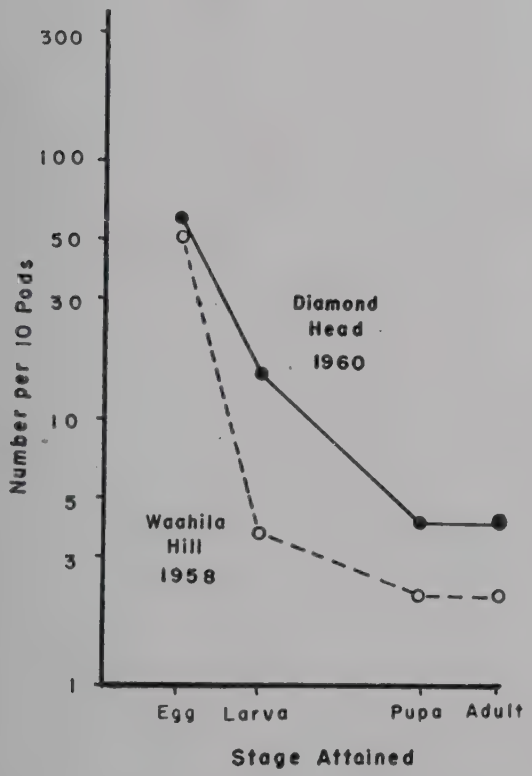

FIG. 2. Survival of *M. sallaei* in Klu.

Egg mortality appeared to be high in both areas. Parasitization by the trichogrammatid wasp, *Uscana semifumipennis* Girault, was of much less importance than either predation or addling. Since addling was not observed under sheltered laboratory conditions, it may have been caused by such physical factors as radiation and desiccation in the field.

Presumably some of the larvae which hatched were unable to penetrate the pod and others drowned in the exudations of green pods or starved in the seeds of moldy pods, but these forms of mortality during the first larval instar could not be measured readily. It was possible, nonetheless, to estimate the parasitization of larvae by dissection of grubs in green seeds, by counts of wasp exit holes in brown seeds, and by rearings (see Hinckley 1960). There was no evidence of pupal mortality in the weekly collections. However, other studies showed that exposed pupae and emerging adults of *M. sallaei* were occasionally attacked by the mite, *Pyemotes boylei.*

The collections of mature klu pods gave information on the parasitization of *M. sallaei* by various wasps at different levels of infestation. Since the competing organisms on klu, unlike those on koa haole, usually acted independently, the percentage of "damaged" seeds could not be regarded as an index of infestation. Instead, infestation was best indicated by those seeds with emergence holes, categorized as "destroyed" by *M. sallaei.* In Table IV, data on competition, infestation, and survival are presented.

TABLE IV. Competition, infestation, and survival of *M. sallaei* in klu pods

Area	% seeds damaged by competitors	Total seeds	% seeds destroyed by M. sallaei	% survival from infestation to emergence
Waahila Hill	39.4	2588	32.4	50
Diamond Head	27.7	2766	51.0	52
Maunalani Heights	28.8	920	31.6	56
Waialae Nui	25.3	941	38.6	54
		7215		
Season				
Summer (Jul.-Sep.)	27.2	2362	48.5	51
Autumn (Oct.-Dec.)	31.1	2418	37.6	47
Winter (Jan.-Mar.)	38.2	1171	21.7	63
Spring (Apr.-Jun.)	27.6	1264	46.4	59
		7215		

Despite temporal and spatial differences in beetle density, survival percentages were usually close to 52%. Detailed records suggest that of the 48% parasitized, the braconids, *Urosigalphus bruchi* Crawford and *Glyptocolastes bruchivorus* Crawford, accounted for 31%, while 2 smaller wasps, a eulophid, *Horismenus* sp., and a pteromalid, *Lariophagus texanus* Crawford, contributed the other 17%. Parasitization by the braconid, *Heterospilus prosopidis* Viereck, and the eupelmid, *Eupelmus cushmani* (Crawford) totaled less than 1%.

The percentages for seeds damaged by competitors were inversely correlated with those for seeds destroyed by *M. sallaei.* This negative correlation is especially noticeable in the summation by seasons. Most of the competitive damage was caused by a fungus, *Aspergillus* sp., and an oletheutid moth, *Cryptophlebia illepida* (Butler).

For comparative purposes, several collections were made of kiawe pods at various points around Honolulu during 1958 and 1959. Of 516 bruchids reared from kiawe, 39.6% were *M. sallaei,* 32.6% *Algarobius prosopis* (Leconte), 25.6% *Mimosestes amicus* (Horn), and 2.2% *Caryedon gonagra* (Fabricius). Comparable collections of klu produced about 1420 bruchids, 98.8% *M. sallaei,* 1.1% *C. gonagra,* 0.1% *M. amicus,* and no *A. prosopis.* There were also conspicuous differences between klu and kiawe in parasite rearings. A total of 427 solitary wasps were reared from klu: 67.1% *Urosigalphus,* 30.9% *Glyptocolastes,* 1.9% *Eupelmus,* and 0.2% *Heterospilus.* Although large numbers of the small, gregarious parasites, *Horismenus* and *Lariophagus,* emerged from the klu pods, few *Horismenus* or *Lariophagus* were reared from kiawe. However, there were 339 solitary parasites; 51.5% *Heterospilus,* 32.4% *Urosigalphus,* 16.0% *Glyptocolastes,* and 0.1% *Eupelmus.*

Despite the high egg mortality of *M. sallaei,* it seems possible that a grub may sometimes enter a seed which is already occupied by another grub. Such situations were easily studied in the laboratory and it was noted that even when 5 grubs penetrated the same seed, only one beetle emerged. To find out how and when the mortality occurred, klu seeds were exposed to *M. sallaei* on September 6, 7, and 8, 1959. Grubs penetrated the seeds about September 15, and on September 22 several seeds were dissected. Two or 3 living larvae were found in each seed. A week later, dissections showed that only one live grub was present in each seed with one or 2 dead and shriveled grubs nearby. Normal adults began emerging from the remaining seeds on October 10.

Presumably the competitive mortality occurred during the 2nd week of larval development, by which time the grubs had attained such a size that contact became quite likely. Those larvae injured by the mandibles of another grub apparently lost their body fluid and died.

Discussion

Weather, competition, and pod maturation

Infestations of *A. levipennis* appeared to be strongly influenced by differing rates of koa haole pod maturation which, in turn, were related to weather conditions. The period from the point at which seeds started to swell until the time at which they browned and began to harden seems to have been as long as 3 weeks during wet weather and as short as one week under dry conditions. Since *A. levipennis* females usually attacked only green seeds, cumulative oviposition was directly related to the duration of the susceptible period. The longer periods of susceptibility were more common at Waahila Hill and during the winter months, the shorter periods at Diamond Head and during the summer. Rates of ripening were of less importance in the determination of *M. sallaei* infestation levels on klu. Oviposition by this bruchid was observed as early as the 5th week of klu pod development and could occur on pods more than a year old.

Weather apparently had both direct and indirect effects on the mortality of beetles. A possible example of direct effects would be the mortality of *M. sallaei* eggs from physical factors associated with exposed situations. Indirect effects, especially those influencing the larval survival of both species, were even more conspicuous.

The collections summarized in Table II and IV showed that infestation by *A. levipennis* was highest and that by *M. sallaei* lowest, under the more humid conditions prevailing during the winter months and in the Waahila Hill area. It should be noted that these infestation records were based on larval rather than egg populations and that high infestations do not necessarily indicate high survival from oviposition to adult emergence. Nonetheless, laboratory studies under wet and dry conditions, as well as comparisons of survival at similar oviposition levels in Waahila Hill and Diamond Head, showed that *A. levipennis* had a better chance of completing its development under moist conditions.

The lower survival of *A. levipennis* under xeric conditions apparently resulted, not from the direct effects of dryness on larvae, but from the changed condition of food. In a dry environment, koa haole seeds hardened quickly and *A. levipennis* grubs usually starved. Frequently, they also starved from the competitive destruction of seeds by microorganisms under moist conditions but, at moderate oviposition levels, their chances of survival on moist and moldy seeds were somewhat greater than on dry and clean seeds. Of course, when the seeds first rotted, then dried, the beetles had virtually no chance of survival.

In the infestations of *M. sallaei* on klu, somewhat different circumstances prevailed. Since the grubs could develop in hard and dry seeds but not in those damaged by fungi, the highest infestations occurred in the xeric environments which favored neither the transmission nor the growth of fungi.

It thus appears that inter-specific competition, especially with fungi, was an important source of mortality for grubs of both beetles under wet conditions. Direct intra-specific competition, however, did not seem to be common either in populations of *A. levipennis* or in those of *M. sallaei.*

Protection, infestation, and larval parasitization

It was noted that solitary koa haole plants usually had light infestations of *A. levipennis* although klu bushes under comparable conditions had moderately heavy infestations of *M. sallaei*. The observed levels of infestation on naturally isolated bushes should be attributed primarily to differences in the oviposition habits of the 2 beetles. *A. levipennis* did not attack brown pods of koa haole but *M. sallaei* oviposited readily on mature pods of klu. Thus, *M. sallaei* populations on isolated klu bushes were able to persist even when green pods were unavailable, whereas populations of *A. levipennis* on isolated bushes usually died out when there was a break in the production of new pods.

High beetle density per pod or area was not correlated with high percentage parasitization. *Pyemotes* and *Eupelmus* together usually killed less than 10% of the *A. levipennis* larvae, even in the heaviest infestations. They were of still less importance as sources of *M. sallaei* mortality. However, in *M. sallaei* populations, other parasites killed approximately 48% of the larvae within seeds at all levels of infestation.

The failure of *Pyemotes* to contribute greatly to larval mortality can be explained by the inaccessibility of the grubs. Normally, the mites did not gain access to koa haole pods until *A. levipennis* adults had begun to emerge. By then, most of the beetles had either died or completed their development and, although the mites could parasitize pupae and teneral adults, their parasitization was not a major source of mortality. Their still lower effectiveness against *M. sallaei* can be attributed to the greater protection afforded the grubs and pupae by the klu seeds.

Physical barriers also limited the effectiveness of the wasps attacking *M. sallaei* larvae. Grubs developing in seeds near the center of a klu pod may have been protected from parasitization, because the ovipositors of such braconids as *Urosigalphus* and *Glyptocolastes* are about 2 mm long and the average klu pod is 10 mm in diameter. With the smaller wasps, *Horismenus* and *Lariophagus*, the physical limitation of oviposition seems even more probable, since their ovipositors are less than one mm long.

The physical barriers limiting the effectiveness of *Pyemotes, Urosigalphus, Glyptocolastes, Horismenus*, and *Lariophagus* seem to have been equally important over a wide range of host densities. For example, grubs of *A. levipennis* in heavily infested koa haole pods were no more exposed to attack by *Pyemotes* than those in lightly infested pods. Furthermore, the proportion of *M. sallaei* grubs in seeds near the center of a klu pod apparently did not change as the infestation gradually increased. Thus, the last grubs infesting a klu pod were no more accessible to wasps than the first.

Other factors must have contributed to the rarity of attacks by *Heterospilus* and *Eupelmus*. The response of *Heterospilus* to plant hosts may be critical, since it appeared to develop readily in the grubs of *M. sallaei* and other bruchids in kiawe. The low parasitization of *Eupelmus* on *A. levipennis* and *M. sallaei* seemed to be related to site conditions and seasonal effects. *Eupelmus* parasitization was highest on both hosts during the winter months and at Maunalani Heights.

Summary

Weekly collections of maturing pods of koa haole, *Leucaena glauca* (L.) Benth., produced evidence that the pods were susceptible to attack by *Araecerus levipennis* Jordan from the time at which seeds started to swell until the time the pods turned brown, a period lasting from one to 3 weeks. The shorter periods were more common under drier conditions, the longer, in wetter situations. Survival of eggs was high in newly susceptible koa haole pods but low in pods of klu, *Acacia farnesiana* (L.) Willd. Larval starvation was frequent on hard seeds in dry pods and on moldy seeds in wet pods.

Mimosestes sallaei (Sharp) could oviposit on any klu pod more than 6 weeks old. Many eggs were removed by predators or killed by physical factors, possibly heat and desiccation. Some larvae of *M. sallaei* starved in klu seeds destroyed by competitors such as the fungus, *Aspergillus* sp., and the olethreutid moth, *Cryptophlebia illepida* (Butler). Counts of emergence holes indicated that parasitization by the braconids, *Urosigalphus bruchi* Crawford and *Glyptocolastes bruchivorus* Crawford, was 31% while that by 2 smaller wasps, the eulophid, *Horismenus* sp., and the pteromalid, *Lariophagus texanus* Crawford, was 17%.

Moist environmental conditions, which favored the growth of competitive organisms such as fungi, were detrimental to both *A. levipennis* and *M. sallaei*. Intra-specific competition between grubs, however, was uncommon in populations of either beetle. Since *A. levipennis* could not develop in hard seeds, it had less chance than *M. sallaei* of maintaining populations in dry environments or on isolated bushes. Physical barriers appeared to limit the effectiveness of parasites attacking grubs of *A. levipennis* and/or *M. sallaei*. There was no evidence that these parasites were either

hampered by the sparsity or aided by the crowding of their hosts.

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STANDING CROP AND DRIFT OF STREAM BOTTOM ORGANISMS[1]

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Stream bottom organisms tend to drift downstream in varying degrees according to species. Since some groups of organisms are particularly susceptible to drifting, this phenomenon must contribute to ecological relationships unique to flowing waters. Several workers have investigated drift in relation to feeding habits of trout (Needham 1929, Ide 1942, Müller 1954). Needham (1928a, b) measured the drift of trout food organisms, where he was primarily interested in the contribution of terrestrial insects. More recently, G. R. Alexander (personal communication) has begun studies on the characteristics of drift in a Michigan trout stream. Yet few investigators have been concerned with the relation of the rate of drift to population density of the bottom organisms or with the role that this mechanism plays in the productive process.

Dendy (1944) apparently first expressed the concept of the drifting of stream organisms as a normal process in streams, even in the absence of floods or abnormal current velocities. Müller (1954), upon studying the drift in streams of northern Sweden, concluded that "in running water a travelling benthos is present as well as, and to the same extent as, the strictly localized benthos. Our observations showed that this travelling benthos (drift) was found during the whole period of the observations and that we must regard it as a constant factor of running water fauna."

Since it appears that the drift of stream organisms is an integral feature of stream ecology, as Dendy and Müller concluded, and is not of negligible proportions, it becomes desirable to determine the significance of drift in relation to population density, level of productive capacity, and many environmental factors.

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The present study was carried out to investigate the standing crop and drift rate of a stream bottom fauna as they may be affected by varying levels of productive capacity.

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Methods

A series of streams was selected which embraced a wide range of expected productivity. Then studies were made of population density and rate of downstream drift of the invertebrate animals in the bottom fauna, with data collected from stations where such environmental factors as current velocity and bottom type were constant among the several streams.

Five streams were selected along the east side of Minnesota, ranging from the rich, limestone streams in the southeast to the relatively poor, soft-water streams north of Lake Superior. These streams, in order of probable decreasing productivity, were: North Branch Creek, Fillmore County; Valley Creek, Washington County; Otter Creek, St. Louis County; Blackhoof River, Carleton County; and Devil's Track River, Cook County. North Branch and Valley creeks lay in relatively fertile soil areas of eroded limestone in the southern and middle portions of the state; the other 3 streams, to the north, lay in less fertile areas which included glacial lake clay or considerable igneous rock. On this basis alone, it would be expected that the northern streams would be less productive than the southern streams, a conclusion generally indicated by trout stream studies

in the state (Smith and Moyle 1944, Johnson 1946, Smith, Johnson and Hiner 1949, R. E. Schumacher, personal communication). Other data including the alkalinity of the stream waters (determined at the time of sampling in 1958) and estimates of trout populations are presented in Table I, upon the basis of which the ranking of expected productivities was made. For example, the relationship between productivity and alkalinity is well known in lakes (Moyle 1949), while Needham (1938) and Armitage (1958) conclude that a similar relationship exists in streams. The sizes of trout populations given in Table I, though no doubt including some sampling error, probably reflect in a general way the capacity of the streams to produce trout food organisms. Trout are also present to some degree in Devil's Track River (Smith and Moyle 1944); in Valley Creek, casual observations and angling reports of landowners indicate extremely high trout populations but no quantitative data are available for these 2 streams.

TABLE I. Available data on trout population density and total alkalinity in 5 Minnesota streams

Stream	Trout population density (pounds per acre)	Total alkalinity[1] ppm
North Branch Creek	111.96[2]	260
Valley Creek	—	220
Otter Creek	9.4[3]	80
Blackhoof River	0.58[4]	75
Devil's Track River	—	23

[1] Total alkalinity determinations made by the author, August, 1958.
[2] Smith, Johnson, and Hiner, 1949.
[3] Data collected by University of Minnesota students at Cloquet Forest Research Center, with assistance of field personnel of the Minnesota Department of Conservation, average of years 1946-1957.
[4] Kuehn, Jerome H. 1951. 1950 Nemadji River Survey, Minn. Dept. Cons., Invest. Report No. 110.

The points of sampling were selected such that the physical characteristics of all streams were similar as to width and depth, current velocity, discharge, and bottom type. Rates of drift of the invertebrate animals were measured with drift nets 1 foot wide and 3 feet long, similar to those employed by Alexander. They were constructed of Nitex (trade mark of Tobler, Ernst & Traber, Inc., New York) with mesh opening of 471 microns, 39 meshes to the inch; consequently only the invertebrates larger than this were captured.

The nets were set in the stream for a period of 1 hour from 10 AM to 11 AM in all instances; 2 samples were collected side by side at each of 2 sites on each sampling date. Each site was located near the downstream end of a riffle at a point where, as near as it was possible to select, the stream width was approximately equal to the average width upstream and where depth and current velocity were reasonably uniform across the stream. To correct for the degree and direction of stream constriction, where it was present, drift rates were computed on the basis of volume of organisms per hour per standard foot of width, a standard foot of width being equivalent to 1 foot of width if the stream width at the sampling site had been exactly equal to the average width.[2]

Standing crop samples of the bottom fauna were collected with a square-foot Surber sampler. Four square-foot samples were collected from the riffle areas above the drift nets after the drift samples had been obtained, on each sampling date.

Sampling was conducted periodically once each 2 weeks during the months of August and September, 1958, for a total of 4 sampling dates, obtaining a total of 16 each of drift and bottom samples from each stream. The animals were sorted in an enamel pan, separated into taxonomic groups, and measured volumetrically by a liquid displacement technique. (One set of drift samples from Valley Creek was inadvertently spoiled for statistical purposes and removed from the presentation of data, leaving 12 drift samples from this stream; the mean of these 4 samples was, however, approximately equal to the mean of the others, and no change in the final conclusions would have resulted.)

The principal groups of organisms present included the crustacean, *Gammarus limnaeus* (in Valley and North Branch creeks only); Ephemeroptera (Heptageniidae in the northern streams only [Blackhoof, Otter, Devil's Track], and Baetidae in all streams); Trichoptera of several families in all streams; Simulidae (Diptera) in all streams; Pelecypoda (*Sphaerium*), important only in Otter Creek; Odonata; large, long-lived Plecoptera (*Acroneuria, Pteronarcys*); and Megaloptera (*Nigronia*), the last 3 in the northern streams only. Of minor importance, volume-wise, there were present other Diptera, including Chironomidae, Ceratapogonidae, Tipulidae, Stratiomyiidae, and Rhagionidae; smaller Plecoptera (*Taeniopteryx*); molluscs; Oligochaeta; Coleoptera; Ephemeroptera (Ephemeridae); and Hemiptera.

RESULTS

Distribution of drift rates

As might be expected the drift was composed principally of organisms which are free-ranging and relatively weak swimmers (Baetidae, [Ephemeroptera] and *Gammarus limnaeus*); few strongly sedentary forms (*e.g., Hydropsyche,*

[2] To compute drift rate in terms of volume per standard foot of width, the average width upstream from the sampling site for about 100 feet (M), and the width at the sampling site (W) were measured. The average of the 2 drift net collections (in milliliters/hour) was then multiplied by the ratio, W/M.

Trichoptera) or strong swimmers (*e.g,* Odonata, Plecoptera) were present in the drift. Organisms of terrestrial origin or flying adults of aquatic immatures which had emerged were not included in the analysis.

The distribution of mean rates of drift among the 5 streams corresponded closely to the ranking of the streams on the basis of expected productivity, except that no significant differences could be noted among the 3 northern streams (Figure 1). At the least, the 2 southern streams, Valley and North Branch creeks, appear immediately distinguishable as having higher drift rates than the northern streams, Blackhoof, Otter, and Devil's Track. This apparent direct relationship of drift rate to level of productive capacity suggests that the drift rate might be employed as an index to the net production rate of a stream bottom fauna (defined as the biomass produced by a bottom fauna, regardless of the fate of the

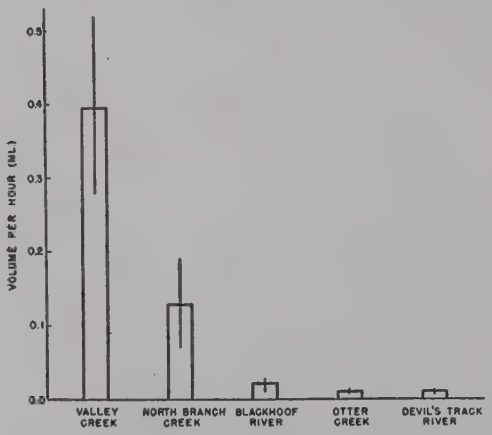

FIG. 1. Mean rates of drift of stream bottom organisms in 5 Minnesota streams, in volume per hour per standard foot of width, during August and September, 1958. Vertical lines represent 2 standard errors on each side of the mean.

group's individual members, per unit time—in the sense used by Clarke (1946).

If this relationship is a valid one, it would appear that the drifting of stream invertebrate animals is a process very intimately associated with production and, as such, may actually be essential for the orderly conduct of stream communities as they have evolved at present. In this regard, Müller (1954), upon studying drift in Swedish streams, proposed the question: What mechanism is employed to prevent upstream areas from being depleted by the drift? For a partial answer to the question, he pointed out several instances in which the flying adults of insects migrate in an upstream direction to lay their eggs, thus is completed the cycle which the immature forms commenced by drifting downstream, and a depletion of upstream areas is prevented. Roos (1957) conducted experiments on the direction of flight of adult stream insects and found females with mature eggs flying in a predominantly upstream direction. Müller (1954) proposed the term "colonization cycle" to describe this series of phenomena. In the case of some organisms which do not have a flying-adult phase, however, he recognized that the question of upstream repopulation was unanswered; he considered this question particularly significant with the crustacean, *Gammarus,* which is observed in the drift in very large quantities.

Müller provides a clue to the question of *Gammarus* and similar organisms in pointing out that a function of drift is to regulate population density. He concluded that drift serves to regulate populations by preventing over-abundance of progeny in the upstream areas as they grow larger and meet increased food and space requirements, and he states that, in addition to mechanical factors such as floods and ice, "the main cause of drift formation lies in the competition between individuals." Therefore, it may be argued that in this function drift must be density-related, and consequently it may not be expected to deplete the upstream areas to population levels less than the carrying capacity. In other words, drift, along with other forms of density-related removal such as predation, is a function of the rate of production. Consequently, some organisms, such as *Gammarus,* may complete their life cycle in the upstream area and furnish sufficient brood stock without the return of adults from downstream.

Following these arguments further, if drift is density-related and a function of the rate of production, it may be postulated that mean rate of drift would be in some constant relation to the mean production rate, provided that such factors as major erosion, floods, and pollution, which might preclude the continuance of a steady-state condition, were absent. This hypothesis is supported by the results of the present study.

The effect of several factors must be evaluated before drift rate may be generally accepted as an index of production rate. First, there are differences among species; some (for example, the molluscs) appear not to drift at all, regardless of their probable production rate. Current velocity is a 2nd factor which has a decided effect upon drift rate, a relation observed in the present study and also reported by Müller (1954). In the 5 Minnesota streams, the sampling sites were selected such that the current velocity was approximately

the same, though it was not measured, in order to minimize possible effects due to such differences. Seasonal fluctuations were observed, however, and unusually high drift rates were invariably associated with recent rains. Probably the best means of minimizing errors from this factor would be to employ a mean computed over a long period of time, preferably a complete year.

Thirdly, seasonal differences in drift rate, perhaps due to seasonal differences in rate of production, should be evaluated. Again, an annual mean would probably be most meaningful. Diurnal differences, too, will be effective; in the present study drift rates were always measured at the same time of day in order to minimize errors from possible diurnal differences. The character of the bottom will no doubt be shown to be a factor affecting drift rate, since the bottom type probably affects production rate, as well as species composition and population density. Temperature, light, and turbidity are other factors, the effect of which upon drift rate should be evaluated.

Distribution of standing crops

The distribution of standing crops among the 5 streams (Figure 2) was not at all similar to the ranking of expected productivities nor to the distribution of drift rates. More specifically, from Fig. 2 (which includes all organisms) the more productive southern streams, Valley and North Branch creeks, cannot be clearly distinguished

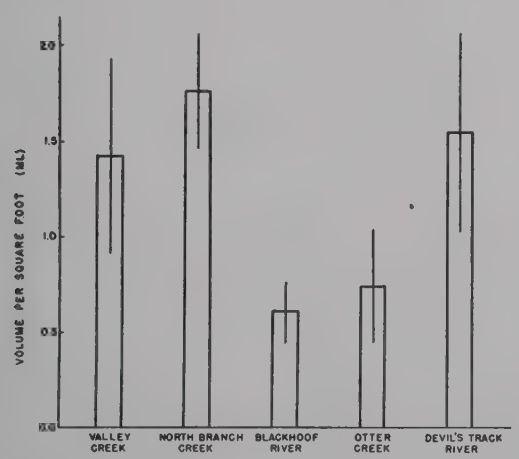

FIG. 2. Mean standing crops of stream bottom organisms in 5 Minnesota streams, all organisms combined (Groups 1, 2, and 3), during August and September, 1958. Vertical lines represent 2 standard errors on each side of the mean.

from the unproductive northern streams. It must be concluded from these data that, at least in general application, total standing crop may not be used as an index to production rate.

A major theoretical objection to the use of standing crop as an index to production rate is that the ratio, standing crop: production rate, must be assumed constant. This assumption will obviously not hold true if there are varying relative quantities of organisms having different longevities. For example, organisms such as the Odonata with a life cycle of several years would be expected to be present in the standing crop to a higher degree relative to their production rate than would organisms such as the Trichoptera which have a shorter life cycle of 1 year. Lindeman (1941) employed this principle correctly in estimating annual production rate of aquatic organisms by multiplying the standing crop by the number of generations per year, even though his procedures were shown by Allen (1951) to be fallacious for other reasons.

To study the effect of longevity upon the distribution of standing crops among the 5 streams, the organisms in the standing crop were separated into 3 groups on the basis of longevity. Information on longevity for many insect groups has been summarized in a general way by Pennak (1953); Embody (1911) presented considerable life history data on *Gammarus limnaeus;* Murphy (1922) and Ide (1935) report 2 or 3 generations for *Baetis vagans* (Ephemeroptera), but it is reasonable to expect similar life histories for other mayflies similar to *Baetis vagans;* Jobbins-Pomeroy (1916) has reported several generations per year for a number of species of Simulidae (Diptera); and Holdsworth (1941) reported a nymphal life of 3 or 4 years for a species of *Pteronarcys,* and Frison (1935) found 2 or 3 years for *Acroneuria* (both Plecoptera).

"Group 1" is composed of organisms which have 2 or more generations per year, namely, *Gammarus limnaeus,* free-swimming Ephemeroptera (Baetidae), and Simulidae. "Group 2" is of organisms of essentially a one-year life cycle, predominantly Trichoptera. "Group 3" is of the greatest longevity; it includes Odonata, long-lived Plecoptera (*Acroneuria, Pteronarcys*), and Megaloptera, all of which have a life cycle of 2 or more years.

If these groups are progressively removed from the standing crop data, starting with the long-lived forms in Group 3—in other words, approaching the condition of homogeneity in respect to longevity—the distribution of standing crops among the 5 streams becomes more and more similar to the ranking of expected productivities and also to the distribution of the drift rates.

In Fig. 2, where all organisms are included, little similarity may be seen to the ranking of expected productivities nor to the distribution of drift rates

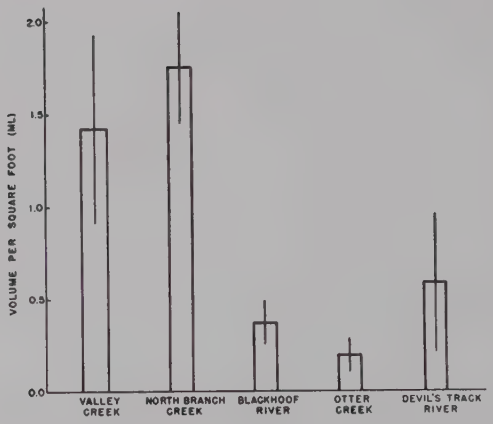

FIG. 3. Mean standing crops of stream bottom organ- in 5 Minnesota streams, Groups 1 and 2, during August and September, 1958. Vertical lines represent 2 standard errors on each side of the mean.

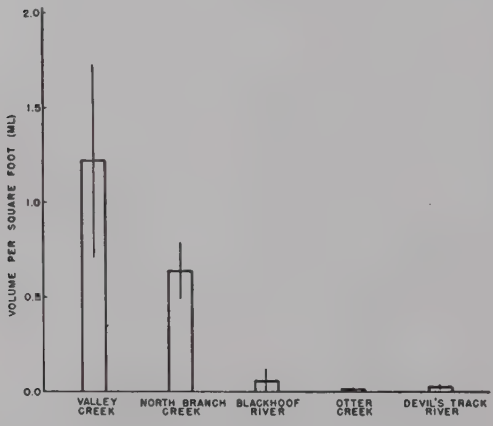

FIG. 4. Mean standing crops of stream bottom organisms in 5 Minnesota streams, Group 1, during August and September, 1958. Vertical lines represent 2 standard errors on each side of the mean.

shown in Fig. 1. In Figure 3, where the long-lived forms are excluded, the similarity is somewhat better, and here at least a clear distinction can be made between the productive southern streams and the relatively unproductive northern streams. In Figure 4, which includes only *Gammarus limnaeus,* free-swimming Ephemeroptera, and Simulidae, the similarity is remarkably close.

It would appear that standing crop is directly related to production rate, but only where groups of similar longevity are compared, or at least where the large long-lived forms are excluded from the standing crop. Where a group or groups of similar longevity may not be present in all situations where comparisons are desired, the stream containing the group of organisms with the shortest longevity may be expected to be the most productive since the rate of removal (which is balanced by production rate) is greater in the case of short-lived organisms.

It is obvious that the greater part of the biomass in the unproductive northern streams is made up of the long-lived organisms, and that in the southern productive streams the short-lived forms predominate. The presence of *Gammarus limnaeus* in only streams of high alkalinity appears to be well documented (Titcomb 1927), and their presence in these streams no doubt contributes greatly to apparently high production rates of trout foods and trout in cold alkaline streams. Where present, the predominance of this form in stream drift and its rapid succession of generations (Embody 1911) would indicate its high production rate. The presence of all ages and sizes at one time would be expected to ensure the most efficient utilization of a species' food resources.

Comparison of drift rate and standing crop as indices of production rate

If drift rate and qualitatively-limited standing crop (limited to groups of similar longevity) may be shown to be equally valid as indices of production rate of a stream bottom fauna, several other factors of a more practical nature should be taken into consideration in judging their relative utility as research tools.

The first of these is that the sampling error in the measurement of drift rate appears to be considerably less than in samples of the standing crop. The extremely large variation in stream bottom samples is, of course, well known. The standard errors of the standing crops shown in Figs. 2, 3, and 4 are minimal since the sampling was restricted to a single habitat, the riffles; if the entire stream bottom had been sampled, with all habitats represented, the variation would no doubt have been greater. The standard errors for the drift rates in Fig. 1, however, are maximal because a considerable amount is due to changes in water level and current velocity and could be removed (*e.g.,* as "Among dates" error) in an analysis of variance. In other words, the process of drift may act as a sort of "mixing process" wherein all productive components of the stream's bottom fauna are reflected in proper proportions in a single measurement—drift rate.

Another practical advantage is the considerably less time and effort involved in analysis of drift samples. Though containing some floating debris, drift samples do not involve large quantities of bottom materials which make sorting of standing crop samples a tedious and expensive process.

Also, for reasons expressed in the preceding paragraph, fewer samples are necessary.

A final advantage of the use of drift samples which may apply in some experiments is that the producing area is not disturbed; in taking standing crop samples the populations may be altered to such a degree that additional samples may not be taken safely for some time.

Summary

The distribution of rates of drift of invertebrate animals among 5 Minnesota trout streams compared favorably with a ranking of expected productivities made on the basis of surrounding geology, water alkalinity, and available trout population data.

The distribution of standing crops of the bottom fauna among the 5 streams was not at all similar to the ranking of expected productivities nor to the distribution of drift rates, until the standing crop samples were qualitatively limited to groups of organisms having similar longevities. When the standing crop samples were limited only to those organisms having 2 or more generations per year, the distribution was similar to the ranking of expected productivities and remarkably close to the distribution of drift rates.

It is postulated that the mean rate of drift of invertebrate animals and qualitatively-limited standing crop may be useful as indices to the production rate of a stream bottom fauna. Of the 2, measurement of drift rate has the practical advantages of smaller sampling error and the need for fewer samples, less effort in sorting and analysis of the samples, and a lack of the undesirable aspect of destroying the producing population.

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A POPULATION SURVEY OF RHESUS MONKEYS IN VILLAGES, TOWNS AND TEMPLES OF NORTHERN INDIA[1]

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INTRODUCTION

This paper presents data on the abundance of rhesus monkeys (*Macaca mulatta* Zimmerman) in villages, towns and temples of Uttar Pradesh in northern India. A total of 310 villages and towns and over 200 Hindu temples were surveyed for the presence of rhesus monkeys during the period, September 1959 until February 1960. Four districts in different parts of Uttar Pradesh (formerly United Provinces) were selected for the survey work: Aligarh in western U.P., Azamgarh in eastern U.P., Banda in southern U.P., and Dehra Dun in northern U.P. (Figure 1). The first 3 are typical districts within the upper and central Gangetic plain. Dehra Dun is at the edge of the Himalayan foothills.

FIG. 1. Map of Uttar Pradesh showing major cities and district centers for village and town surveys (underlined).

The state of Uttar Pradesh is located in the north-central portion of the range of the rhesus monkey in India. This range is usually described as extending from western Kashmir through Nepal to Assam and Burma, and south to the rivers Tapti (150 miles north of Bombay) in the west, and Godavari (100 miles north of Hyderabad) in the east (Pocock 1939, Prater 1948). This description needs revision, however, since the rhesus is reported to be common around Hyderabad (Rae, personal communication). In southern India, the rhesus is replaced by the Bonnet monkey (*Macaca raditata* Geoffroy).

Uttar Pradesh is commonly considered to be an area of high rhesus monkey abundance. Sixty to 70% of the rhesus monkeys trapped for export purposes are obtained from Uttar Pradesh (Rae, personal communication).

This paper is the first of two on rhesus abundance throughout Uttar Pradesh. The subsequent paper will present a survey of roadside habitats, canal banks, railroad rights-of-way, and forest areas. These several types of survey were designed to sample all the major rhesus monkey habitats in northern India.

Villages were selected as logical starting points in the population survey since villages have often been mentioned as major habitats for rhesus monkeys (Jerdon 1874, Prater 1948). In addition, villages present one of the most prominent ecological features of northern India. They contain all essential environmental factors of adequate monkey habitat: trees, water, food, and shelter. One or more of these factors may be absent in the terrain between villages. Hence many plant and animal communities in northern India are oriented with respect to villages, and some species appear to have population centers located in villages. We considered it possible that this might be true of rhesus monkeys.

Temples were also selected as logical starting places for the rhesus population survey since monkeys have been traditionally associated with Hindu temples (Mann 1938). Unlike villages, however, temples are neither definable nor discreet units. They vary greatly in size, from tiny cubicles in crowded bazaars to extensive park-like areas in open country. Some have local water supplies and groves of trees, others have neither of these features. Some temples are used daily and have permanent human inhabitants, others are abandoned. Hence the word "temple" cannot refer to any specific type of habitat unless certain arbitrary definitions are applied. In this survey, attention was largely confined to temples with at least ¼ acre of grounds, a water supply available to monkeys, and a grove of trees on the temple grounds.

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The objects of this population survey were: (1) to obtain data on the abundance and distribution of rhesus monkeys in Uttar Pradesh, (2) to obtain data on group sizes and group structures in terms of sex and age ratios, and (3) to estimate trends in the rhesus populations.

Essentially no data have been published on any of these topics. A recent paper by Nolte (1955) on the Bonnet monkey (*Macaca radiata* Geoffroy) of southern India enumerates many aspects of basic knowledge about the abundance, distribution and ecology of Indian monkeys on which no studies have been conducted and for which no references are available. Personal communications with zoologists in India, government officials, and commercial monkey exporters indicated that no general population surveys of rhesus abundance and distribution have been conducted[3]

Population data on rhesus abundance and distribution are of potential value in at least 3 fields of applied ecology. In the first place, population data could assist in evaluating the rhesus populations of India as possible reservoirs of human diseases. Rhesus monkeys are susceptible to a wide range of infectious diseases which are identical with or similar to many human diseases. These include bacterial, virus, spirochaetal, rickettsial, protozoan and helminthic infections. Rhesus could theoretically play a role in the endemiology or epidemiology of such diseases. For example, the dengue fever virus or the relapsing fever spirochaete might conceivably be arthropod borne from monkeys to man. Other diseases such as bacillary dysentery, leptospirosis, or dracontiasis might be transmitted from monkeys to man through contaminated water or food. Laboratory studies of rhesus monkeys have also shown susceptibility to several diseases which are not currently known in India. These include yellow fever, St. Louis encephalitis, Japanese B-encephalitis, and Rift Valley fever (Manson-Bahr, 1954). Should these viruses gain entry into India, they could conceivably become reservoired in rhesus monkey populations. In the Bonnet monkey of southern India, a new and serious virus disease of man known as Kyasanur Forest Disease (Work *et al.* 1957), is tick-borne from monkeys to man. An adequate understanding of the epidemiology of this disease requires some information on the abundance and ecology of the Bonnet monkey.

Secondly, population data could assist in evaluating the role of rhesus monkeys as agents of agricultural crop destruction. Rhesus monkeys are frequently seen feeding upon sugarcane, wheat, gram, pulses, millets, and vegetable crops. The extent of monkey depredations cannot be estimated without data on abundance.

Thirdly, population data on rhesus monkeys could help to evaluate the supply for export. The United States has recently required between 200,000 and 300,000 monkeys per year for programs of vaccine production and medical research, and the majority of these have been obtained from India. Reports from commercial rhesus exporters in 1959 suggested that they were finding increasing difficulty in obtaining sufficient numbers of monkeys to meet the demand. This paper is not intended to explore any of these applied fields but to supply population data upon which further investigations may be based.

Description of the Area

The state of Uttar Pradesh lies in north central India, extending from 24° to 31° north latitude and from 77° to 84° east longitude. It is composed of approximately 113,410 square miles, of which 79% are alluvial plains of the Jumna, Ganges & Ghaghara rivers, 5% are upland plateau, 6% are Himalayan foothills, and 10% are Himalayan mountains.[4]

Approximately 65% of the total land area of U.P. is under cultivation. The major crops in decreasing order of acreage are wheat, rice, gram, barley, mustard, millet, pulse, sugar cane, corn, ground nuts, potato and cotton.

Forest areas in U.P., largely in foothills and mountains, compose 14% of the total land area. The remaining 21% of the land area consists of fallow land, barren uncultivable land, alpine areas, urban areas, roadways, railroads, canals and miscellaneous land-use categories.

The human population of U.P. is currently estimated at about 75,000,000. The population density in 1951 was 557 people per square mile. Eighty-six % of the population was rural.

A recent enumeration listed a total of 108,941 villages in U.P. with less than 2000 people each. Sixty-nine % of these villages have populations of less than 500 people, 21% have 500 to 1000 people, and 10% have from 1000 to 2000 people.

There are 3,267 towns and cities in U.P., and of these, 86% have populations from 2,000 to

[3] Personal interviews were held with Dr. B. C. Mahendra, President, Academy of Zoology (of India); Dr. G. C. Pandit, Director, Indian Council of Medical Research; Mr. M. S. Rae, Director, Vita Private Ltd.; Shri Ranganathan, Undersecretary, Ministry of Agriculture and Fisheries and Secretary of the Indian Board of Wildlife; and Dr. Harold Trapido, Deputy Director, Virus Research Centre. Correspondence was conducted with Dr. M. L. Roonwall, Director, Zoological Survey of India.

[4] The geographic and demographic data in this section have been obtained from the Statistical Abstract of India, 1955-56, published 1957 by the Central Statistical Organization, Cabinet Secretariat, Government of India, New Delhi.

5,000 people, 9% have from 5,000 to 10,000 people, and 5% are towns and cities with more than 10,000 people. The major cities of U.P., and their 1951 census estimates are Kanpur (705,383), Lucknow (496,861), Agra (375,665), Benaras (355,777), and Allahabad (332,295). Smaller cities in U.P. in the range of 100,000 to 250,000 are Aligarh, Bareilly, Dehra Dun, Gorakhpur, Jhansi, Mathura, Meerut, Moradabad, Saharanpur, Shahjahanpur and Sitapur. Delhi, the largest city in northern India, is politically distinct from U.P., but the Delhi area is geographically and ecologically similar to western U.P.

The climate varies considerably. The winter season, from October to early March, is warm in the day throughout the plains (60° to 80°F) and cool at night (40° to 50°F). In the Himalayan foothills and mountains, it is much colder, with snow in many regions. The summer season from late March until June, is hot and dry in the plains with day temperatures exceeding 100°F in May and June, and night temperatures ranging from 60° to 80°F. In the foothills and mountains, more moderate temperatures prevail. The monsoon season, extending from July to September, is hot and humid, with temperatures usually in the range of 80° to 95°F night and day throughout the plains. In the foothills and mountains more moderate temperatures again prevail. Rainfall is almost confined to the monsoon with the exception of a few scattered winter rains. The annual rainfall averages 30 to 50 inches in the plains, and 40 to over 100 inches in the foothills and mountains.

Methods

The numbers of villages and towns surveyed in each of 4 different districts of Uttar Pradesh are shown in Table I. These were randomly selected within a 35-mile radius of each district center, except that approximately 70% of the villages in each district sample had populations of less than 500 people, approximately 20% had populations from 500 to 1,000 people, and 10% had populations from 1,000 to 2,000 people. Likewise, the town survey was conducted randomly with the exception that approximately 85% of the towns within each district had populations from 2,000 to 5,000, and 15% had populations from 5,000 to 15,000. This sampling pattern was selected to agree with the actual pattern of village and town size distribution throughout Uttar Pradesh.

There is some ecological basis for distinguishing between villages and towns at the population level of about 2,000 people. Communities above 2,000 people usually have bazaar areas, commercial areas and moderate to large-sized temples, whereas smaller villages rarely have any of these features.

Table I. Incidence of rhesus monkeys in villages and towns of Uttar Pradesh

Districts	No. of villages or towns surveyed	No. with resident monkeys	Aver. no. of groups per village or town	No. with monkeys as occasional visitors	Additional no. of villages or town which had monkeys in last five years
Village survey:					
Aligarh (Western U. P.)	108	12 (11%)	1.0	12 (11%)	11 (10%)
Azamgarh (Eastern U. P.)	50	16 (32%)	1.0	8 (16%)	9 (18%)
Banda (Southern U. P.)	69	10 (14%)	1.8	22 (32%)	14 (20%)
Dehra Dun (Northern U. P.)	53	6 (11%)	1.3	13 (24%)	5 (9%)
Total	280	44 (16%)	1.25	55 (20%)	39 (14%)
Town survey:					
Aligarh	16	11 (69%)	2.3	1 (6%)	3 (19%)
Azamgarh	9	6 (67%)	2.0	2 (22%)	0
Banda	5	4 (80%)	5.7	0	1 (20%)
Total	30	21 (69%)	2.78	3 (10%)	4 (13%)

A survey consisted of walking around the village, through its major alleyways, inspecting most of its trees, and examining its water supply for evidence of monkeys. In addition, we questioned many villagers at 2 or 3 places to ask if monkeys were present, if monkeys ever came to the village, and if monkeys had been present within the last 5 years. These conversations were all in local Hindi or Urdu dialects, and we feel moderately confident about the information obtained. Finally, the village survey included a cursory inspection of fields, gardens, woodlots, and mango groves surrounding the village.

In towns, procedures were much the same, but less intensive. We could often drive through parts of the town and look for monkeys from the automobile. We again questioned people about monkeys and were usually directed to the place where monkeys could be found.

If monkeys were found, the villagers were questioned as to whether the monkeys had been present within the last 5 years or whether they had recently come. Some time was then spent with the group of monkeys to obtain a sex and age count. This was easy if we happened to find the monkeys all feeding together or undergoing definite group progression from one location to another, but it was sometimes impossible if the monkeys happened to be widely dispersed and were sleeping or grooming. In such cases we attempted to return to the village in early morning or late evening to obtain a reliable count.

Individuals were grouped into the following categories: (1) adult males, (2) adult females,

(3) infants, and (4) juveniles. Infants were identified as young when generally dependent upon the mother, unweaned, and usually carried by the mother during group progression. Infants were definitely less than 4 pounds in body weight, and were judged to be less than one year old. Such individuals frequently moved some distance from the mother during play or feeding, but most of the time they remained closely associated with the mother.

Juveniles were identified as young which were largely independent of the mother, definitely weaned, and more than 4 pounds in body weight. They were judged to be more than one year of age and less than 4. Occasionally, borderline individuals were seen and an arbitrary judgment was made. If the individual was seen to ride upon the female, or was seen to nurse successfully, it was classified as an infant.

Juveniles were distinguished from the adults by their smaller size and lack of red sexual skin. Both of these characteristics are highly variable, however, and subjective judgments were necessary on many occasions.

The temple survey could not be organized on a definite program of sampling, since temples could not be defined or classified as satisfactorily as villages and towns. Throughout the travel associated with the village and town survey, hundreds of temples were inspected. Particular attention was given to those with at least ¼ acre of grounds, a grove of trees and a water supply available to monkeys. Temples of this sort were usually found in large towns. Questioning of local people usually led us directly to such temples and often to temples where monkeys were known to be. Occasionally, monkey groups were found which visited small temples frequently during part of their normal daily movements, but which usually inhabited some other location. Such groups were not considered temple groups. Only groups which usually slept and obtained most of their food within the temple grounds were considered temple monkeys. Even these monkeys, however, would not necessarily be confined to temple grounds, and they might take excursions into surrounding areas.

Results

Village and town monkeys in relation to geographical region

The incidence of village and town monkeys in relation to geographical region is shown in Table I. Of the 280 villages sampled throughout all 4 districts, 16% possessed resident monkey groups (all of which had apparently been there for at least 5 years), an additional 20% reported that monkeys came into the village occasionally, and an additional 14% reported that monkeys had been present within the last 5 years, but were no longer present. Five years ago, nearly 30% of the villages had resident monkey groups. The average number of monkey groups per village with resident monkeys varied from 1.0 in Aligarh district to 1.8 in Banda. The maximum number of groups per village occurred in Kamta, a large village in Southern U.P. where 5 groups were seen.

The region with the greatest incidence of resident monkeys was eastern U.P. around Azamgarh, where 32% of 50 villages surveyed had resident monkeys. This is a significantly higher incidence of village monkeys than that occurring in the total sample of 4 regions ($\chi^2 = 10.062$; $P = < 0.02$). Southern U.P. in Banda district, however, showed the highest percentage of villages which reported monkeys as occasional visitors (32%; $\chi^2 = 9.728$; $P = < 0.03$). Banda district also showed the highest percentage of villages which had had monkeys within the last 5 years (20%; $\chi^2 = 3.809$; $P = > 0.25$). Thus, eastern U.P. had the highest incidence of resident village monkeys, while southern U.P. had the highest incidence of transient village monkeys. Village monkeys were more abundant in both of these regions than in western and northern U.P.

Towns have monkeys more frequently than villages. Over 68% of 30 towns sampled in 3 regions showed resident monkeys, an additional 10% indicated that monkeys came as visitors, and another 13% indicated that monkeys were present within the last 5 years but had been driven away or trapped. Hence, 5 years ago, approximately 80% of the towns in this sample probably had rhesus monkeys present. Southern U.P. in Banda district showed the highest percentage of towns with resident monkeys (80%), but only 5 towns were sampled. The average number of rhesus groups per town with resident monkeys varied from 2.0 in Azamgarh to 5.7 in Banda. The maximum occurred in Chitrakut, a small town in Southern U.P. where 10 groups were seen.

The size and structure of village and town groups in relation to geographical region is shown in Table II. In 50 village groups, the average group size was 17.4, with 3.5 adult males, 7.2 adult females, 4.6 infants, and 2.0 juveniles.

Towns exhibited larger group sizes with an average of 22.4 composed of 4.4 adult males, 9.7 adult females, 5.9 infants, and 2.4 juveniles. This is not significantly larger than the village group however ($\chi^2 = 0.643$; $P = > 0.30$). The smallest groups in villages or towns consisted of a single adult pair. Solitary males were seen on 4

TABLE II. Group structure of rhesus monkeys in villages and towns of Uttar Pradesh (Mean ± standard error)

District	Group size	Adult		Sub-adult		Sample size (No. of groups)
		♂♂	♀♀	I I	J J	
Village survey:						
Aligarh (Western U. P.)	13.4±1.9	3.2±0.5	5.8±0.8	4.2±0.7	0.2±0.1	10
Azamgarh (Eastern U. P.)	16.2±1.9	3.1±0.4	6.4±0.9	4.5±0.8	0.9	14
Banda (Southern U. P.)	18.2±2.0	37. ±0.4	7.9±0.9	4.3±0.4	2.3±0.3	18
Dehra Dun (Northern U. P.)	25.1±2.3	4.4±0.5	9.1±1.0	6.1±0.9	5.5±0.7	8
Total	17.4±1.2	3.5±0.2	7.2±0.5	4.6±0.3	2.0±0.4	50
Town survey:						
Aligarh	24.4±6.1	4.0±0.9	10.0±2.3	6.7±1.6	3.9±2.1	9
Azamgarh	13.4±3.3	2.7±0.5	6.0±1.4	4.6±1.3	0.1	7
Banda	24.3±3.1	5.1±0.8	10.7±1.4	6.0±0.8	2.4±1.8	23
Total	22.4±2.5	4.4±0.5	9.7±1.1	5.9±0.7	2.4±0.5	39

occasions but were not counted as groups. The largest village or town group observed consisted of 57 monkeys seen in the town of Khair in Aligarh district. A group of 78 individuals inhabiting a temple in Hathras is not included in this category since Hathras is a town of 50,000 people. This group is included in the temple survey.

In villages, the largest average group size (25.1 individuals) occurred in the Dehra Dun sample. This is significantly larger than the average group sizes of Aligarh (13.4), Azamgarh (16.2), or Banda (18.2), when these 3 are grouped together and considered as a single population ($\chi^2 = 5.474$; $P = < 0.02$), but it is not significantly larger than the total sample mean of all 4 districts ($\chi^2 = 3.407$; $P = > 0.05$). The Dehra Dun sample is also unusual in that it showed the highest number and percentage of juveniles (22%) among the village samples ($\chi^2 = 8.195$; $P = < 0.05$).

In the town samples, Aligarh and Banda showed an average group size of 24.4 and 24.3 individuals respectively, but Azamgarh showed a smaller group size of 13.4. This difference does not quite attain significance at the 5% level ($\chi^2 = 3.611$; $P = > 0.05$).

The percentages of males, females, infants and juveniles in the population samples are shown in Table III. The population compositions of village and town monkeys were very similar; approximately 20% adult males, 42% adult females, 26% infants, and 11% juveniles.

Some regional variations in population composition did occur, particularly in the proportion of juveniles. The percentage of juveniles varied from 1% in the towns of Azamgarh to 22% in the villages of Dehra Dun. This is interpreted as an indication of trapping pressure, and is discussed later.

TABLE III. Population composition of rhesus monkeys in villages and towns of Uttar Pradesh

District	Sample size (No. of monkeys)	Percentage Adult		Percentage Sub-adult	
		♂♂	♀♀	I I	J J
Village survey:					
Aligarh	134	23.9%	43.3%	31.3%	1.5%
Azamgarh	207	20.8	43.0	30.4	5.6
Banda	327	20.5	43.4	23.5	12.5
Dehra Dun	201	17.4	36.3	24.4	21.9
Total	869	20.4	41.6	26.6	11.4
Town survey:					
Aligarh	220	16.3%	40.7%	27.2%	15.8%
Azamgarh	94	20.2	44.7	34.0	1.1
Banda	559	21.2	44.1	24.7	10.0
Total	873	19.8	43.2	26.4	10.5

Village and town monkeys in relation to community size

The incidence of monkeys in relation to village and town size is shown in Table IV. Large villages and towns had a significantly higher incidence of resident monkeys than small villages ($\chi^2 = 27.521$; $P = < 0.01$). Only 14% of small villages showed resident monkeys as compared with 18% of medium-sized villages, 22% of large size villages, 58% of small towns, and 91% of medium towns. A significant relation to community size was likewise shown in the number of communities which reported monkeys within the last 5 years. Only 10% of small villages reported monkeys within the past 5 years compared to 31% of large villages ($\chi^2 = 11.870$; $P = < 0.01$).

The largest decline in resident monkeys was in large villages, in which monkeys were apparently

TABLE IV. Incidence of rhesus monkeys in villages and towns of Uttar Pradesh in relation to village and town size

Village and Town Size	No. of villages or towns surveyed	No. with resident monkeys	Aver. no. of groups per village or town	No. with monkeys as occasional visitors	Additional no. of villages or towns which had monkeys in last five years
Small villages <500	194	27 (14%)	1.1	41 (21%)	19 (10%)
Medium villages 500-1000	54	10 (18%)	1.6	9 (17%)	10 (18%)
Large villages 1000-2000	32	7 (22%)	1.3	5 (16%)	10 (31%)
Small towns 2000-5000	19	11 (58%)	2.4	2 (10%)	4 (21%)
Medium towns 5000-15000	11	10 (91%)	2.7	1 (9%)	0
Total	310	65 (21%)	—	58 (19%)	43 (14%)

resident in more than 50% five years ago, whereas only 22% had resident monkeys in 1959.

The percentages of each community type which reported monkeys as occasional visitors showed an inverse relationship to community size but the differences are not statistically significant ($\chi^2 = 1.699$; $P = > 0.75$). This may reflect the probability that transient monkeys would be more conspicuous in small villages than in large communities. The average number of rhesus groups per community with resident monkeys showed an increase with community size from 1.1 groups per small village to 2.7 groups per medium town.

Group structures in relation to community size are shown in Table V. Large villages and towns had larger group sizes than small villages, but the differences are not significant by the Chi-square test ($\chi^2 = 0.643$; $P = > 0.30$). The smallest average group size, 14.3 individuals, occurred in medium villages. No ecological significance can be attributed to this.

TABLE V. Group structure of rhesus monkeys in villages and towns of Uttar Pradesh

District	Group size	Adult		Sub-adult		Sample size (No. of groups)
		♂♂	♀♀	I I	J J	
Small villages..... pop'<500	18.0±1.6	3.5±0.3	7.2±0.6	5.1±0.5	2.2±0.5	26
Medium villages... 500-1000	14.3±2.6	3.2±0.5	6.3±1.6	3.3±0.6	1.5±0.4	15
Large villages..... 1000-2000	20.6±2.3	4.1±0.5	8.9±1.1	5.5±0.7	2.1±0.6	9
Small towns..... 2000-5000	23.2±3.6	5.0±0.8	10.2±1.6	6.1±1.0	1.9±0.4	22
Medium towns.... 5000-15000	21.3±1.7	3.8±0.5	9.0±1.2	5.6±0.7	2.9±1.2	17
Total.....	19.6±1.3	3.9±0.3	8.3±0.6	5.2±.03	2.2±0.3	89

Temple monkeys

A survey of more than 200 temples of moderate to large size revealed 15 resident groups in 12 different temples. These are fully listed in Table VI. This list obviously does not represent a thorough survey of temples in U.P. nor does it represent a random survey. We specifically visited temples which were most likely to have monkeys, but we undoubtedly missed many groups.

Temple groups exhibited an average size approximately twice that of village and town groups ($\chi^2 = 16.034$; $P = < 0.01$). Groups averaged 41.9 individuals, composed of 7.9 adult males, 15.2 adult females, 9.5 infants, and 9.3 juveniles. The smallest temple group consisted of 16 individuals, the largest of 78 individuals.

Temple groups also exhibited the highest consistent percentages of juveniles (22%) found in this study. This is twice the proportion (11%) of juveniles found in village and town groups ($\chi^2 = 60.785$; $P = < 0.01$). In temple groups, 45% of all monkeys observed were subadult whereas in the village and town groups only 37% were subadult. The reproductive rates of both types of groups were similar as indicated by the infant/adult-female ratio of 62% in village-town groups compared to 63% in temple groups.

TABLE VI. Group size of temple monkeys in Uttar Pradesh

Location	Group size	Adults		Sub-adult	
		♂♂	♀♀	I I	J J
Aligarh—Achal Tank, Group 1..	51	12	14	6	19
" —Achal Tank, Group 2..	34	7	10	8	9
Benaras—Durga Temple.....	46	7	14	8	17
" —Sarnath Temple.....	31	5	11	7	8
Chitrakut—Jagvedi Akhara Temple.....	78	17	35	20	6
" —Bara Math Temple.	26	5	11	6	4
" —Bara Math Temple.	32	9	13	7	3
Delhi—Temple at Hindan Bridge	21	5	9	6	1
Hardwar—.....	34	6	10	7	11
Hathras—Gr. 1.....	49	11	16	14	8
" —Gr. 2.....	74	11	28	16	19
Kamta—Mukharbind Temple..	28	6	14	4	4
Lucknow—Temple at Monkey Bridge.....	54	9	18	13	14
Mathura—Gr. 1	55	6	18	16	15
" —Gr. 2.....	16	2	7	5	2
Total.....	629	118	228	143	140
Means.....	41.9	7.9	15.2	9.5	9.3
s. e.....	±4.6	±0.9	±1.9	±1.3	±1.5
Population Composition.....		18.7%	36.2%	22.7%	22.3%

The adult sex ratios were similar in both types of groups, with approximately twice as many adult females as adult males (47.4 adult males per 100 adult females in village and town groups; 51.8 adult males per 100 adult females in temple groups). This is a common demographic characteristic of primates (Carpenter 1942).

Discussion

Abundance and regional distribution

The rhesus monkey is less abundant in villages and temples of northern India than is commonly thought. Such popularly written statements as . . . "vast hordes of rhesus still roam large parts of India . . ." (Sanderson 1957) and ". . . in the United Provinces alone (Uttar Pradesh) the monkey population—in my opinion—is not less than ten million monkeys . . ." (Corbett 1953), are not appropriate in the light of 1959 population status. Corbett's statement may have been reasonably accurate when it was first written, particularly if it was intended to include langurs or black-faced monkeys (*Semnopithecus entellus* Dufresne) which are particularly abundant in the forest of northern U.P. Corbett's concept of abundance still prevails,

however, and has been applied solely to the rhesus. We have been told by several eminent zoologists of India that there are between 10 and 20 million rhesus monkeys in Uttar Pradesh but no scientific reference for this statement can be found. We cannot give reliable estimates of the monkey population of U.P., but it is inconceivable that the figure could be as high as 10 million. Such a population would mean one monkey for every 7 or 8 people. This ratio might conceivably be approached in a few small localities, but it is very definitely not true for all of U.P. We would venture a guess at the total rhesus population of U.P. as on the order of 800,000 to 1,000,000. Probably more than half of these would be in village and town habitats.

Concerning the pattern of regional distribution, eastern U.P. around Azamgarh had a significantly higher incidence of village monkeys (32% of the villages surveyed had resident monkeys) than the other districts of U.P. which were sampled (11% to 14%). This, we feel, is probably due to more favorable attitudes of the villagers toward monkeys, and to better habitat in eastern U.P.

Interview data indicated that a higher percentage of villagers in eastern U.P. have tolerated and protected monkeys than in other regions. The interview data also indicated that this practice of protection is changing rapidly. Many villagers reported that they had protected the monkeys until the last year or two, but that they were now permitting them to be trapped or were driving them out of the village. Human attitudes and practices toward the monkeys are important factors in determining the patterns of abundance and distribution, and changes in these attitudes are playing key roles in determining population trends of the rhesus. This topic is developed more fully later.

We also feel that the greater incidence of village monkeys in eastern U.P. is attributable to superior habitat. Central and eastern U.P. have greater numbers of preferred food trees than other regions. This cannot be documented quantitatively, but is an impression gained while traveling through the countryside. Some of these preferred food trees are: banyan (*Ficus bengalensis* L.), pipal (*Ficus religiosa* L.), fig. (*Ficus carica* L.), mango (*Mangifera indica* L.), neem (*Melia azadirachta* L.), imli or tamarind (*Tamarindus indica* L.), jaman or jambo (*Eugenia jambolana* Lam.), and sheesham (*Dalbergia sisso* Roxb.).

The greater number of rhesus groups per village and town which were found in the Banda district is probably a sample artifact. Two villages, Kamta and Khohi, and one town, Chitrakut, which have unusually large numbers of monkeys, occurred in this sample. These are places of Hindu pilgrimage, and monkeys have been traditionally fed and protected around temples and sacred places. In the town of Chitrakut, for example, a community of approximately 2,500 people which is an important religious site in Hindu mythology, 10 groups of rhesus monkeys were found. This was a very unusual abundance for a small town.

Northern U.P. has more extensive forest and jungle areas, but these are not dominated by preferred food trees for rhesus monkeys (see Champion 1936). The forests of northern U.P. do represent excellent protective cover for rhesus monkeys and, quite possibly, the significantly larger group size exhibited by the Dehra Dun village groups can be attributed to this excellent cover. The Dehra Dun groups frequently ranged out into forest areas and tea estates surrounding the villages. They were wild and shy in their behavior, and were probably more successful in avoiding trapping than village monkeys in the plains.

Group size

The factors influencing group size are complex but probably fall into 3 categories. Environmental factors such as the availability of food, water, trees and protective cover are undoubtedly important. One would expect that an abundant and well distributed food supply in a highly structured habitat would tend to produce a larger group size than a sparse and concentrated food supply in a simple habitat. There might be many complicating factors, however, and this entire subject of environmental influences upon group size requires further study.

Secondly, human attitudes and human behavior toward the monkeys are determinants of group size. The fact that temple monkeys had an average group size of 41.9 individuals compared to 19.6 individuals for village and town monkeys is suggestive of this factor. But environmental differences of the type mentioned above make a simple explanation impossible.

A 3rd group of factors influencing group size are behavioral characteristics of the monkeys. Observations indicated definite tendencies, particularly male dominance patterns, which undoubtedly influence group size. There are indications of central grouping tendencies which are fairly characteristic of primates (Carpenter 1942, 1953). Evidence of group fission appeared in small groups of 12 or 14 monkeys and, in large groups of 40 to 50 monkeys, there were signs of subgrouping tending toward new group formation. The point at which fissioning occurred was again related to certain features of the habitat. This topic will be discussed more fully in a subsequent paper on the social behavior of temple groups.

Population trends and human interactions

Two aspects of the data indicate considerable recent decline of the rhesus populations in villages of Uttar Pradesh. Interview data revealed that 30% of 280 villages surveyed had resident monkeys 5 years ago. In 1959, only 16% had resident monkeys. The decline has been particularly evident in medium and large-sized villages, where the decline in 5 years was approximately 50% to 60%. This does not necessarily mean that monkey populations have declined to this extent because it is possible that many groups have been driven from villages and towns to roadside or canal bank habitats. It is our opinion, however, that most of the decline in village monkeys has involved actual population decline rather than a shift in habitat distribution. At least, we could find no habitat category in which a detectable increase in rhesus had occurred.

The age structure data also indicated declining populations. Reproductive rates were high, as evidenced by the fact that approximately 60% of the females in village, town and temple groups were carrying infants. In all samples obtained, however, except temple groups and Dehra Dun village groups, the percentages of juveniles were considerably smaller than the percentages of infants. In 2 outstanding cases, the villages of Aligarh and the towns of Azamgarh (Table III), the percentages of juveniles in the populations were less than 2%, while those of the infants were over 30%.

This indicates a serious loss of juveniles. In normal primate age structures there should be at least as many juveniles as infants (Collias and Southwick 1951, Carpenter, Mason and Southwick 1960). The only samples attaining this condition were temple groups and Dehra Dun village groups.

Temple groups possess a certain incomplete immunity from trapping and molestation. We have met monkey trappers in temple grounds, where they were apparently observing the movements of the monkeys out of the temple area to discover if they might be trapped. Usually, however, temple groups are not trapped to the extent of village and town groups. As previously mentioned, the Dehra Dun village groups were probably more successful in escaping trapping than village monkeys in the plains, because of the superior forest cover available to them. This could account for both their larger group size, and the higher percentage of juveniles.

Trapping for export is directed largely against the juveniles. During the period of this study, approximately 14,000 juvenile rhesus monkeys per month were being exported from New Delhi (Rae, personal communication). Most of these were juveniles in the weight range of 4 to 6 pounds, and approximately one to 2 years of age. To obtain this number of monkeys monthly, trappers work throughout the range of the rhesus monkey from Kashmir to Assam, and south almost to Hyderabad (Rae, personal communication).

Some trapping is also directed against adult monkeys. In certain cases this is done for specific research requirements, but usually it is done to rid an area of all monkeys. Several villagers told us that they gave permission to obtain monkeys only on the stipulation that the trappers would take all monkeys including adults. In many cities of Northern India, the municipal governments hire trappers to get rid of nuisance monkeys. In New Delhi considerable adult trapping has been done in recent years, but some groups of monkeys around government buildings have successfully eluded all trapping attempts. These are largely old adults.

In general, this intensive trapping program has resulted in an effective removal of juveniles. The adult breeding stock is not being adequately replaced to maintain stable populations.

Additional factors which we believed to be important in the decline of rhesus populations in northern India are changing attitudes among villagers. The monkeys in villages and temples of northern India have existed largely through traditional care and protection from the people. In many villages the monkeys are no longer receiving this traditional protection. Villagers frequently told us that they had driven groups of monkeys out of the village, or had encouraged trappers to come. A few villagers indicated that they had actually killed monkeys, which are now considered destructive and bothersome animals.

There are probably many reasons for these changing attitudes. One is the acute competition for food which now exists in India. Most villagers with whom we spoke are not willing to watch monkeys consume their crops and food supplies when their own children are hungry. A 2nd reason of probably equal importance is the changing pattern of Hindu customs quite apart from simple population pressure. Traditional social and cultural patterns in India are undergoing rapid change. The attitudes towards monkeys are simply one small part of much broader cultural changes occurring in India.

The religious status of the rhesus monkey is complex and variable. In classical Hinduism, the rhesus monkey is not sacred (Lydekker 1893, Pocock 1939), while the langur (*Semnopithecus*

entellus Dufresne) is definitely considered a sacred animal. The monkey god, Hanuman, which plays a very important role in Hindu mythology, was similar to a langur, but a specific distinction between langurs and macaques is apparently not made in the minds of many devout Hindus. In everyday religious practice, therefore, all monkeys probably enjoy some degree of sacred status. Hence, Hindu holy places such as Mathura, Chitrakut, Hardwar and Benaras all have large numbers of monkeys. They are well protected and fed within the confines of temples and sacred places, but if they make excursions away from such places they may be subjected to trapping and molestation. The religious practices of the villagers seem to be greatly simplified in comparison to many town and temple dwellers. Hinduism does not require that villagers feed and protect rhesus monkeys as a religious practice.

Summary

This paper presents data on the numbers of rhesus monkeys found in villages, towns, and temples of Uttar Pradesh in northern India during the period of September 1959 to February 1960.

A survey of 280 villages in 4 different regions of U.P. indicated that 16% possessed resident monkey groups, 20% reported that monkeys came to the villages occasionally, and an additional 14% reported that monkeys had been present within the last 5 years, but were no longer present.

The region with the greatest abundance of resident village monkeys was eastern U.P. around Azamgarh, where 32% of the villages had resident groups. This might be attributed to the more abundant distribution of preferred food trees and to more extensive protection of the monkeys by villagers. The practice of protection is changing rapidly, however.

A survey of 30 small and medium-sized towns indicated that 69% of them had resident monkey groups, 10% reported that monkeys came as occasional visitors, and an additional 13% reported that resident monkeys had been present within the last 5 years but were no longer present.

Within 5 years there has apparently been a 47% decline in the number of villages with resident monkeys and a 16% decline in the number of towns with resident monkeys.

In 50 village groups the average number of monkeys was 17.4, composed of 3.5 adult males, 7.2 adult females, 4.6 infants and 2.0 juveniles.

In 39 town groups, the average group size was 22.4, composed of 4.4 adult males, 9.7 adult females, 5.9 infants and 2.4 juveniles. Village and town monkeys had similar population compositions with approximately 20% adult males, 42% adult females, 26% infants, and 11% juveniles.

The largest average group size of village and town monkeys occurred in the sample of village monkeys observed around Dehra Dun in northern U.P. Here the average group size was 25.1, and contained 22% juveniles. This is considered a reflection of superior cover available to the monkeys in the forests and jungles of northern India.

The data indicate that resident monkey groups occurred in 14% of small villages, 18% of medium-sized villages, 22% of large villages, 58% of small towns, and 91% of medium-sized towns. Although large villages and towns tended to have larger groups than small and medium villages, the differences were not significant.

A survey of more than 200 Hindu temples revealed only 15 resident groups of rhesus monkeys in 12 different temples. This was not a random sample of temples, since a specific effort was made to inspect temples that would be most likely to have monkeys.

Temple monkeys exhibited an average group size twice that of village and town monkeys: 41.9 individuals, composed of 7.9 adult males, 15.2 adult females, 9.5 infants, and 9.3 juveniles. Temple groups showed a significantly higher percentage of juveniles (22%) than any of the village or town groups except the Dehra Dun village sample. This is attributed to the fact that temple monkeys are not trapped as intensively as village and town groups.

In village groups, town groups, and temple groups, the infant/adult-female ratio was approximately 60%. The adult sex ratios were also similar in the 3 types of groups, varying from 47.4 adult males per 100 adult females in village and town groups to 51.8 adult males per 100 adult females in temple groups.

Interview data and age ratio data indicated that the rhesus populations of Uttar Pradesh are declining. This is attributed to intensive trapping for export purposes and to changing attitudes of villagers in northern India. Monkeys are neither protected nor fed by the majority of villagers.

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FOOD ENERGY AVAILABLE FOR AND REQUIRED BY THE BLUE GROUSE CHICK[1]

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Introduction

This study is concerned with the importance of food to the blue grouse chick and represents a portion of a larger and continuing investigation of factors affecting the abundance of blue grouse *Dendragapus obscurus fuliginosus* (Ridgway) on Vancouver Island, British Columbia. An introductory study undertaken in 1943 by Fowle (1960) presented information on life history and summer food habits of the blue grouse. Since then a study by Bendell (1954, 1955) has shown the influence of parasitism on a population at a relatively high density.

The coastal blue grouse characteristically become abundant on large newly-burned areas. Bendell (1954) suggested that this increasing density may be explained primarily as the result of an abundance of the invertebrate food supply for the chicks, and from the change in the structure of the vegetation following a forest fire. On the other hand the lack of invertebrate food, independently, or together with inclement weather has been advanced as a factor partially responsible for mortality of galliform chicks by several authors, notably Bump *et al.* (1947), Edminster (1947), Criddle (1930), and Stokes (no date). Lack (1954) also presented evidence that food is limiting the numbers of certain birds.

The purpose of this study was to measure the amount of invertebrate food available to the blue grouse chicks during their first few weeks of life. By relating this to the quantity of food required by the chicks, the importance of food could be assessed as a factor influencing the number of chicks that could be supported on a given area.

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Methods

The investigation was carried out in the spring and early summer of 1958. The area of study lies 12 miles to the southwest of Campbell River, Vancouver Island, and consists of 30,000 acres which were burned in 1951. Two study plots of 40 acres each, hereafter referred to as A and B, were selected on the relatively homogeneous burn.

The diet of blue grouse chicks is composed almost entirely of invertebrates during their first few weeks of life (Beer 1943). In order to measure the amount of invertebrate food available to the blue grouse chicks, it was necessary to sample the habitat periodically for invertebrates living within a defined "zone of availability." This has been described by Edminster (1947) for the ruffed grouse chick as extending from the loose ground litter to a height of one foot above the earth. This was accepted as applicable to the blue grouse chick. Sampling was undertaken in a manner to simulate the circumstances under which chicks acquire their food as they pick up exposed invertebrates. The sampling technique consisted of searching along a strip of ground one foot wide for 5 minutes, the time being arbitrarily chosen. The rate of advance along the strip should not influence the yield over an area unless a speed of coverage beyond the scope of rapid vision is exceeded. All invertebrates within the zone one foot in width and one foot in height were collected in an aspirator, killed in cyanide and dried. To convert the average abundance of invertebrates per 5 minutes to abundance per area, 10 samples were taken and the distance moved during each was measured. This gave an average distance of 45.2 ± 0.98 (95% confident limits) feet. Thus the area covered during each sample was 45.2 ± 0.98 ft^2. The required number of samples to be collected each day to give minimum variation between samples was estimated by taking a series from each of the 2 plots. It was found that from 6 to 10 samples give an allowable error of 15%. Sampling was confined principally to the morning hours with occasional sampling during mid-day and evening. All invertebrates of each sample were identified to order. Each sample was then dried at 80°C to constant weight and weighed to the nearest tenth of a milligram.

Since the chicks change to a predominantly vegetarian diet after the first 2 weeks, a quantity of the more important plant foods was collected and preserved for analysis of nutrients.

The gross chemical composition as well as the quantity of foods was measured. Both invertebrate and plant foods were analyzed for crude protein, ash, ether extract (crude fat) and total carbohydrate as recommended by Official and Tentative Methods of Analysis (1950). Total carbohydrate was estimated by taking the difference between 100 and the sum of protein, ether extract, and ash. The nutrient fractions of the carbohydrate, namely crude fiber and nitrogen-free extract, were not determined analytically because of a lack of material. However, they were estimated in the following manner and should be considered as approximate only: For invertebrates the ratio of these 2 carbohydrate components was taken from that reported for the same invertebrate groups by Birge (1922), Phillips and Brockway (1954), Embody and Gordon (1924), and Beck and Beck (1955). For plants the carbohydrate components were estimated by plotting the percentage of protein against crude fiber for a large number of plants including all of those collected for analysis. Thus for a determined value of protein the corresponding value of crude fiber could be read. The carbohydrate composition of the plants was obtained from Miller (1958), Russel (1947), Schneider (1947), Spinner and Bishop (1950), and Beck and Beck (1955). The average digestibility of the nutrients was estimated from Titus (1949) by averaging separately the digestibility figures for the plant and animal foods listed. However, arthropods possess a cuticle partially composed of chitin which is indigestible in vertebrates. Tsao and Richards (1952) report the average amount of chitin in several representative insects as 6 and 4% for adults and larvae respectively (per total dry weight). This indigestible portion was substracted from the total digestible nitrogen-free extract for each food. The digestible portion of each nutrient for both plant and animal foods was then multiplied respectively by 4, 9, and 4 (protein, fat, carbohydrate) to give the total metabolizable energy value for each food (Ewing 1951).

The determination of the energy and feed requirements of the chicks during their first 4 weeks of life was accomplished by the use of the factorial method described by Mitchel *et al.* (1930, 1931) and Maynard and Loosli (1956).

Results

Invertebrate food

Sampling for invertebrates began on the last week of May and continued into the first week of July. A series of 8 samples taken during the morning of May 23 (7:30) and compared to a series of 10 taken during the evening (8:00) of the same day indicated that no significant differ-

ence existed between the numbers of invertebrates at these times. Members of the order Orthoptera were collected in the samples but excluded in the calculations since none occurred in the crops of the chicks.

The weights of the samples were grouped by weeks and by plots. When the samples within each week are graphed as frequency distributions, the symmetry of a normal distribution was lacking. However, when each succeeding pair of values were summed for each week (any remaining value discarded), an improved normal symmetry appeared. These adjusted data were used for the subsequent computations. Table I shows the average daily weights of invertebrates by weeks from May 25 to July 5 on plots A and B. Since every 2 consecutive values were summed the average weight is now expressed per 10 minutes or per 90.4 ± 2% square feet.

TABLE I. Daily mean dry weights of invertebrates during weeks from May 25 to July 5 expressed as milligrams per 10 minutes or per 90.4 square feet

Weeks	Plot A		Plot B	
	Mean weight	Samples	Mean weight	Samples
May 25-31	52.9±10.9	15	47.6±18.9	9
June 1-7	48.1±16.5	6	55.4±17.4	11
June 8-14	64.5±22.9	10	88.2±22.6	10
June 15-21	47.6±15.7	12	77.2±16.7	12
June 22-28	—	—	84.7± 6.6	3
June 29-July 5	33.0±13.6	2	—	—
Mean (May 25-June 21)	53.2± 8.0	43	67.1±11.3	42

To test whether the differences in the mean weights for each week are real or due to sampling error, the weight data for the first 4 weeks were subjected to an analysis of variance. Significance was established at the 0.01 probability level due to the large variation about the means for each week. The results of the analysis indicate that the differences between the weeks are not significant, but probably are due to sampling error. Therefore averages are calculated for the first 4 weeks for each plot and presented at the bottom of Table I. In addition, when the averages for each plot are compared, there appears to be no significant difference between them at the 0.01 probability level ($t = 2.02$) although this is borderline.

An attempt was made to test the reliability of the invertebrate sampling method as a technique for estimating the amount of animal foods available to the blue grouse chicks. This may be done by comparing the frequency of occurrence of the respective invertebrate groups in the samples with that in 19 crops collected on and about the study area during the month of June (11 collected in 1958 by Stiven and 8 in 1952 by Dr. Bendell). The results of this comparison are presented in Table II. The "crop" column gives the number of crops containing a particular invertebrate group expressed as a percentage of the total number of crops. In the "total daily sample" column the unit is the total daily sample rather than the crop. This is defined as the total number of samples in one particular day, plots A and B combined.

TABLE II. Comparison of percentage frequency of occurrence between the chick crops and invertebrate samples, plots A and B

Animal	Percentage Frequency of Occurrence	
	Crops (June 1-July 5)	Total daily sample (May 25-July 5)
CRUSTACEA		
Isopoda	40	38
INSECTA		
Homoptera	50	100
Hemiptera	5	8
Coleoptera	25	31
Formicidae	90	94
Diptera	20	69
Lepidoptera	5	31
ARCCHNIDA	10	100
MYRIAPODA	5	13
Unidentified Larvae	60	21

This comparison indicates that the sampling method was fairly reliable for estimating the abundance of the major animal foods available to the blue grouse chicks. However, one major group, the unidentified larvae, did not occur as frequently in the samples as it did in the crops. In fact, chicks were finding larvae twice as often as the sampling observer. Other groups such as the Acachnida, Lepidoptera, Diptera, and Homoptera, occurring more frequently in the samples than in the crops, suggested that the efficiency of the sampling observer with respect to these groups was probably slightly better than that of the chicks.

Nutrient analysis of the chick foods

The average digestibility of the animal and plant foods as estimated from Titus (1949) is given in Table III.

The results of the proximate analysis and the estimates of the digestible portion of each nutrient category of each invertebrate group are presented in Table IV.

The average metabolizable energy of the invertebrate foods on a moisture-free basis is 3.11 ± 0.10 kilocalories per gram. Converting to a value expressive of the invertebrates in a fresh state

TABLE III. Average percent digestibility in the chicken of products of animal origin and of green feeds (from Titus 1949)

Nutrient category	Animal foods	Plant foods
Protein	85	65
Fat	84	55
Nitrogen-Free Extract	66 (adult insects) 68 (larvae)	65
Crude Fiber	20 (from Crampton, 1956)	32

TABLE IV. Proximate analysis of invertebrates from Plots A and B in percent dry weight. Nitrogen-free extract and fiber estimated

Animal	Nutrient Composition*					Digestible Portion			
	P	EE	NFE	F	Ash	P	EE	NFE	F
Isopoda	62.8	2.9	19.1	9.2	6.0	53.4	2.1	12.6	1.8
Homoptera	73.3	3.8	9.8	9.8	3.3	62.2	3.2	6.5	2.0
Coleoptera	70.6	4.6	17.6	4.1	3.1	60.0	3.9	11.6	0.8
Formicidae	66.8	2.9	23.7	4.0	2.6	56.8	2.4	15.6	0.8
Diptera	60.9	3.4	23.8	5.9	6.0	51.7	2.9	15.7	1.2
Arachnida	73.9	2.9	16.8	3.0	2.4	62.8	2.4	11.1	0.6
Larvae	76.5	6.4	6.0	6.0	5.1	65.0	5.4	4.1	1.2

* P=crude protein, NFE=nitrogen-free extract, EE=ether extract, F=crude fiber.

yields 0.91 kcal/gm. (The average moisture content of insects is roughly 65% according to Spector 1956). This calorific value for the invertebrates is much lower than that of the artificial chick starters which are around 2.2 kcal/gm and contain about 10% moisture.

The results of the nutritional analysis of the plant foods are given in Table V. The average metabolizable energy of the plants (dry weight) is 2.18 ± 0.02 kcal/gm and as fresh material 0.57 kcal/gm (these plants were found to contain on the average 74% water).

TABLE V. Nutrient composition and estimated digestibility of plant foods in percentage dry weight. Crude fiber and nitrogen-free extract estimated

Plants	Nutrient Composition*					Digestible Portion			
	P	EE	NFE	F	Ash	P	EE	NFE	F
Salix spp. (lvs)[1]	8.8	2.6	60.2	21.0	7.4	5.7	1.4	39.1	6.7
Hypochaeris radicata (lvs)	10.9	4.4	50.8	18.0	15.9	7.1	2.4	33.0	5.8
(fls)	14.4	5.4	53.5	14.0	12.7	9.4	3.0	34.8	4.5
Gaultheria shallon (fls & frt)	9.2	2.0	63.8	20.0	5.0	6.0	1.1	41.5	6.4
Mahonia nervosa (frt)	12.5	1.7	62.4	16.0	7.4	8.1	0.9	40.5	5.1
Rubus spp. (frt)	13.4	1.4	64.3	15.0	5.9	8.7	0.8	41.8	4.8
Pteridium aquilinum (fronds)	12.9	2.4	49.2	27.0	8.5	8.4	1.3	32.0	8.6
Senecio spp. (lvs)	10.9	6.1	51.1	18.0	13.9	7.1	3.4	33.2	5.8

* P=crude protein, EE=ether extract, NFE=nitrogen-free extract, F=crude fiber.
[1] lvs=leaves, fls=flowers, frt=fruit.

These results show, in addition to the lower protein content of the plant foods, a smaller metabolizable energy value of the plants, principally due to their greater moisture content. This indicated that a chick would obtain less useful energy per gram of plant food than it would per gram of invertebrate food.

Energy and food requirements of the chicks

Little appears to be known about the basic energetics of wild galliforms. Most of the experimental nutritional studies have been concerned with the domestic fowl—the few studies on wild galliforms being directed towards improving the quality of feeds (Skoglund 1940) or determining the influence of various nutrients on production and survival (Nestler 1946, Norris *et al.* 1936). Hence the following determination of the minimum energy requirements of the blue grouse chick will be based on the present knowledge of the energetics of the domestic chick.

The daily metabolizable energy requirements of an animal of a given weight are considered to be the sum of the energy required for basal metabolism, plus the energy required in food utilization or the Specific Dynamic Energy (these latter two together are considered as resting metabolism, see Brody 1945), plus the energy required for both activity and growth (Maynard and Loosli 1956). The resultant figure divided by the metabolizable calorific value of the food consumed, gives a value representing the minimum daily food intake of the animal.

The average weekly weights of 3 male and 3 female blue grouse chicks captured on the study area and successfully raised by Mr. and Mrs. G. Gibson of the Department of Zoology, University of British Columbia are considered representative for purposes of calculating the energy requirements.

Kibler and Brody (1944) measured the resting metabolism of growing chickens and found the following relationship between body weight and metabolism:

$$Y = 0.22\,X^{0.98} \text{ (males)} \quad \ldots\ldots\ldots\ldots\ 1$$

$$Y = 0.21\,X^{1.00} \text{ (females)} \quad \ldots\ldots\ldots\ldots\ 2$$

where Y = resting metabolism in kcal per day and X = body weight in grams. The relationship held only during the chick's first 4 weeks of age. These equations are assumed to represent approximately the resting metabolism of blue grouse chicks.

Mitchell *et al.* (1930, 1931), in assessing the energy requirements of domestic chickens, found that the energy expended for muscular activity ranged between 43 and 52% of the expenditures for basal metabolism (the relationship between

basal metabolism and weight was calculated for the first four weeks as $Y = 0.167 X^{1.01}$ from raw data in a paper by Mitchell *et al* (1927). Crampton (1956) supports these estimates for the activity increment. Accordingly the activity requirement for the blue grouse chick has been taken to be 50% of the basal requirement.

The energy requirement for additional tissue growth has been estimated from the daily rate of growth of the chicks (this was found to be 8.6% per day during the first 4 weeks) and from an approximation of the chemical composition of the weight gain obtained from Mitchel *et al* (1931). For example, a chick weighing 32.7 grams gains 2.8 grams per day, of which 21% is dry matter, 15% is protein, and 4% fat. Knowing that 5.65 and 9.4 kcal respectively are required to put on one gram of protein and fat (Brody 1945), the total kcal required for this gain can be computed (3.2 kcal). However this represents the net requirement for growth which is about 70% of the metabolizable requirement (Brody 1945). Therefore 4.6 kcal are necessary for the growth fraction.

The total metabolizable energy requirements for a blue grouse chick during its first 4 weeks are given in Table VI.

TABLE VI. Calculated metabolizable energy and food requirements of one chick based on the average growth of six pen-raised blue grouse chicks

Age (days)	Weight (grams)	Energy Requirements (kcal/day)						Food Requirements (gm/day)		
		Basal	Resting	Activ.	Net growth	Total growth	Total metabol.	Starter	Total fresh	Fresh inverteb.
H-7	32.7	5.4	6.8	2.7	3.2	4.6	14.1	6.4	15.5	15.5
8-14	63.6	10.5	13.1	5.3	6.4	9.1	27.5	12.5	32.4	27.5
15-21	116.8	20.0	23.9	10.0	13.4	19.2	53.1	24.1	61.1	53.8
22-28	195.3	36.6	39.8	18.3	23.1	33.0	91.1	41.4	130.1	46.8

The calculated daily food intake (both natural food and a turkey starter fed to the pen-raised chicks, the latter from B and K Feeds, Vancouver, and having a metabolizable value of 2.2 kcal/gm) is also presented in Table VI. To calculate the quantity of fresh food eaten by the chicks, an appreciation of the crop contents and their calorific value is required. Hence it was found that the average metabolizable energy value of all foods eaten during the first week was 0.91 kcal/gm for the 2nd week 0.85, for the 3rd week 0.87, and for the 4th week 0.70.

To test the validity of the feed intake calculations, a comparison of the consumption of starter between the blue grouse (calculated) and the pheasant (actual intake, from Skoglund 1940) is given in Figure 1. The feed intake during the first 3 weeks is similar for the 2 species. The difference in the 4th week may be partially accounted for by the difference in average weights at this time; blue grouse—195 grams, and pheasant—170 grams (Skoglund 1940). For additional support of the calculations the estimate of 6.5 grams per day for the first week compares favorably with the feed intake of the domestic chick (45 grams per week per chick).[2]

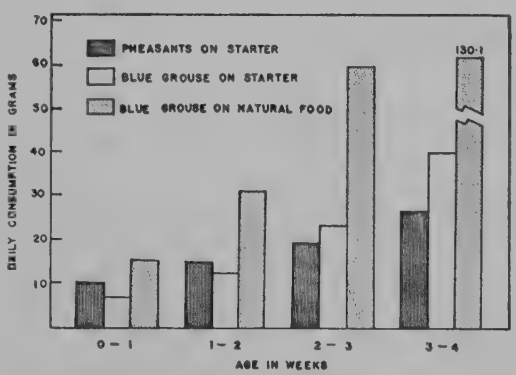

FIG. 1. Comparison of daily food consumption between a pheasant and a blue grouse chick during their first four weeks of life. (Pheasant data from Skoglund 1940).

DISCUSSION AND CONCLUSIONS

By periodically sampling the study plots for invertebrates, the abundance of animal foods available to the blue grouse chick has been estimated (Table I). In addition the quantity of invertebrate food required by the chick during its first 4 weeks has also been determined (Table VI). Therefore an attempt is now made to evaluate the adequacy of the study area for the maintenance of chicks with respect to the invertebrate food supply. Table VII depicts a comparison between these 2 estimates. One approach in determining the potential capacity of the study area for chicks would be to divide the amount of food present by the amount required by one chick. Hence the last column of the table gives a hypothetical estimate of the average potential carrying capacity of the

[2] Personal Communication with Mrs. B. E. March, Dept. of Poultry Science, University of British Columbia.

TABLE VII. Estimated carrying capacity of study plots assuming complete utilization of food

Age of chick (days)	GRAMS FRESH INVERTEBRATES PER ACRE		Fresh invertebrates requir./day (gm/chick)	POTENTIAL NO. OF CHICKS PER ACRE	
	A	B		A	B
1-7	73.4±11	92.1±16	15.5	4.7	6.0
8-14	"	"	27.5	2.7	3.4
15-21	"	"	53.8	1.4	1.7
22-28	"	"	46.8	1.6	2.0

study plots for chicks. This approach, however, assumes complete utilization by the chick of the estimated amount of available invertebrates and is probably unrealistic.

The following approach is more realistic: The average amount of invertebrates on plot A is 73.4 ± 11 grams per acre. This estimate, varying within the 11 gram limit, is present, according to the results of sampling, at any point in time during the first week. During the same time one chick requires an average of 15.5 grams per day or a total of 109 grams by the end of the first week. We will assume that the chick can acquire this amount in one day. Since several chicks do inhabit each of the study plots it must be realized that a certain quantity of invertebrates is being taken from the plots each day and that possibly a portion of this amount would not be accounted for in the samples. The amount taken, of course, would depend on the population of chicks. Moreover, since the quantity of invertebrates appears to be the same at the end as at the beginning of the week, it would seem that the consumption of the invertebrates by the chicks, plus the invertebrates eaten by other birds and rodents, and also those invertebrates succumbing to other causes of mortality, must be in total an amount either equal to or less than the amount of invertebrates produced on the study plots during that week. If the density of chicks averages 0.5 chicks per acre (a rough estimate based on daily observation of study plots) this means a food intake of roughly 8 grams per day for the first week, 14 grams for the 2nd week, and so on, thus indicating an increasing rate of production of invertebrates. If these areas were barren of predators of invertebrates, it would be reasonable to conclude that the quantity of invertebrates would be greater at the end of the week than at the beginning. Similarly, if the population of chicks was appreciably greater, one would expect that the quantity would have been reduced by the end of the week. Therefore the estimated amount of invertebrate food shown in Table VII may be considered to be the 'capital stock' on the study plots.

It appears, therefore, that the amount of invertebrate food, both production (the exact quantity being unknown) and the 'capital stock,' is quite adequate for the present population of blue grouse chicks inhabiting the study area. Of course this conclusion does not take into account the adverse effect of weather that possibly would tend to limit the activity of invertebrates and hence abundance (Talbot 1946, Uvarov 1931), and to limit the time available to the chicks for feeding.

SUMMARY

1. The relationship between early foods and the energy requirements of the blue grouse chick has been studied on a 7-year-old burn, Vancouver Island, British Columbia.

2. The average weight of invertebrates available to the chicks was relatively constant during the time chicks were feeding almost exclusively on animal matter.

3. The major invertebrates and plants eaten by the chicks were collected and analyzed for their basic nutrients, and the average metabolizable energy values for both plants and invertebrates were calculated.

4. The metabolizable energy and food requirements of the chick were determined by the factorial method (partitioning of the component energy requirements) and from reference to the basic energetics of the domestic chick.

5. Disregarding the effects of extreme weather conditions, it appears that the abundance of invertebrates is sufficient to maintain the present population of chicks on the study area.

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TROPHIC SPECTRUM OF AN ESTUARINE COMMUNITY, BASED ON STUDIES OF LAKE PONTCHARTRAIN, LOUISIANA

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One of the fundamental questions in aquatic ecology is the problem of community nutrition. Several recent investigators have achieved a high degree of success in working out quantitative aspects of primary production in natural aquatic communities, but the problems of secondary production (or consumer "assimilation" as Odum 1959 has put it) have not yielded results of the same consequence. This has been due to the absence of any really good methods of analyzing consumer nutrition on a quantitative basis and to the innate complexity of the nutritional relations among the consumer species. Although classical methods might be expected to yield estimates of importance, such studies have usually been more restricted in nature. With a few notable exceptions, comprehensive data regarding the nutrition of a large share of the consumers of a given aquatic community have not been available, and overall patterns of the trophic relations among consumer species have not been well understood.

Several years ago (June, 1953-May, 1955) I participated in an ecological survey of Lake Pontchartrain, a large estuary of the Louisiana coast (Darnell 1954). As part of this study the food habits of 35 of the most important consumer species were investigated in a direct effort to achieve a more thorough understanding of the problem of consumer nutrition and its relation to primary production in a very complex natural community. The results of the food studies of the various species have been published (Darnell 1958), and the present work is an attempt to interpret these results in the context of the total community. The distribution, life history, and general ecological relations of a number of the important food species

have been discussed previously (Crowell and Darnell 1955, Darnell 1959, Darnell and Williams 1956). A brief treatment of the physical environment will be given as a background for the discussion of community nutrition. Names of fish species are in accord with the list of Bailey *et al.* (1960).

Physical Environment

The geologic history of Lake Pontchartrain has been investigated by Fisk (1944, 1947a, b), Steinmeyer (1939), and others. These studies indicate that since its formation the Lake Pontchartrain basin has undergone extensive filling due to the inflow of materials from adjacent environments. Most significant in this respect have been Mississippi River overflow, sedimentation by north shore streams, subaquaeous delta formation at mouths of passes, encroachment by marginal marsh and swamp, and offshore deposition of much humus from the marsh and swamp areas. All of these forces are currently active, and some, at least, may play major roles in community nutrition.

The hydrographic conditions of this estuary have been discussed elsewhere (Darnell 1958). Of particular significance here is the fact that the waters are highly turbid, average Secchi disc visibility being only about 4 feet. The great turbidity was found to be directly related to wind action which disturbs and raises the bottom sediments, even in the deepest water (18 ft). Areas of greatest turbidity were located near eroding shores, especially along the southern margins of the lake.

Nutrition of Larger Consumers

The chief purpose of the present work is to distinguish and clarify the really fundamental nutritional relationships of the estuarine community. Less important side issues have already been discussed in connection with the food habits of the individual species (Darnell 1958). As revealed in the stomach analyses, most consumers appear to ingest food on the basis of ecologic rather than taxonomic association. The major food groupings as distinguished by the consumers themselves appear to include the following: phytoplankton, vascular plant material, zooplankton, micro-bottom animals, macro-bottom animals, free-swimming fishes, and organic detritus.

Components of the major food categories are listed in Table I. In this table a distinction is made between those forms which frequently contributed to a particular food category (primary components) and those which appeared less often or only occasionally (secondary components). To my surprise, the decision between primary and secondary classification for a given component was seldom difficult to make. This clearly reflects the fact that regardless of taxonomic diversity (over 300 species were recognized from this estuary), intensive predation centered around only a few key species. The utilization of each of these major food categories will be taken up separately.

Phytoplankton as a source of food

Stomach contents of the fishes and larger invertebrates seldom included phytoplankton organisms, and in only a few cases was the percentage of this material considered to be significant. Diatoms were sometimes encountered although, as indicated in Table I, the surface-floating blue-green algae were taken in greatest quantity. *Microcystis* was consumed to some extent, but the great bulk of this material was made up of several species of *Anabaena*. Although seasonal in occurrence, these blue-greens were sometimes extremely abundant and were utilized readily by the striped mullet and the young menhaden (for which they apparently formed over 4/5 of the ingested material). The threadfin shad, which strains its food, may also make some use of the blue-green algae. Food of the larvae and very young of most species was not studied, and phytoplankton may have been of direct importance for those forms with pelagic larvae, especially the clupeids, engraulids, and atherinids.

Nutrition of the zooplankton will be discussed in a later section. As far as the larger consumers of the community are concerned, however, direct consumption of phytoplankton was quite low.

Vascular plants

As revealed in the stomach analyses the most frequently consumed vascular plants were *Ruppia maritima* and *Vallisneria spiralis*. Several species of filamentous algae were often taken in together with the vascular plant material, and these forms are best considered together (see Table I).

In a few of the fish species, notably the sparids, vegetation made up a large portion of the diet, as in the sheepshead (54%) and in the adult pinfish (6 to 48%). Vegetable material also constituted up to ¼ of the food of such clearly omnivorous forms as the blue catfish. Many additional species, including even the most carnivorous forms, frequently had consumed some identifiable vegetation. When present in small quantity such material was assumed to have been obtained incidental to other feeding.

The importance of marginal vegetation in the economy of the lake community is exaggerated in the present study by the fact that many of the fishes chosen for food analysis were of necessity taken in shallow water seine hauls, and bottoms which were best for seining frequently were those containing some vegetation. Many of the preda-

TABLE I. Components of the major food groups in the Lake Pontchartrain community based upon stomach analysis of the chief consumer species. The "Organic Detritus" category is of necessity based partly upon circumstantial evidence regarding availability (see text)

Major Food Groups	Primary Components	Secondary Components
Fishes	largescale menhaden *(Brevoortia patronus)* bay anchovy *(Anchoa mitchilli)* Atlantic croaker *(Micropogon undulatus)* striped mullet *(Mugil cephalus)*	ladyfish *(Elops saurus)*, threadfin shad *(Dorosoma petenense)*, "young clupeids" (mostly *Brevoortia patronus*), sea catfish *(Galeichthys felis)*, speckled worm eel *(Myrophis* sp.*)*, pipefish *(Syngnathus* sp.*)*, sheepshead minnow *(Cyprinodon variegatus)*, mosquitofish *(Gambusia affinis)*, sailfin molly *(Mollienesia latipinna)*, tidewater silverside *(Menidia beryllina)*, seatrout *(Cynoscion* sp.*)*, black drum *(Pogonias cromis)*, naked goby *(Gobiosoma bosci)*, bay whiff *(Citharichthys spilopterus)*
Macro-bottom Animals	subadult blue crabs *(Callinectes sapidus)* adult mud crabs *(Rithropanopeus harrisii)*	adult clams *(Rangia cuneata)*, adult penaeid shrimp *(Penaeus aztecus, P. setiferus)*, grass shrimp *(Palaemonetes* spp.*)*, river shrimp *(Macrobrachium ohione)*, mud shrimp *(Callianassa jamaicense)*, adult blue crabs *(Callinectes sapidus)*
Micro-bottom Animals	small rangia clams *(Rangia cuneata)* mussels *(Mytilopsis leucopheata)* isopods and amphipods (many species) small crabs (blue crabs and mud crabs) insect larvae (Chironomidae)	benthic protozoans (esp. foraminiferans), sponge *(Spongilla lacustris)*, hydroid *(Bimeria franciscana)*, small gastropods (Amnicolidae), ostracods, harpacticoid copepods, polychaetous annelids
Zooplankton	calanoid copepod *(Acartia tonsa)* adult schizopods *(Mysidopsis* sp.*)* larval penaeid shrimp *(Penaeus* spp.*)*	protozoans (esp. tintinnids), rotifers, cyclopoid and calanoid copepods, larval forms (mollusks, annelids, crustaceans, and fishes)
Phytoplankton	*Anabaena* spp.	*Microcystis* sp., *Chaetoceros* spp., *Coscinodiscus* spp., *Melosira* sp., and others
Vascular Plant Material	none	*Ruppia maritima*, *Vallisneria spiralis*, and some filamentous algae also included in this category *(Cladophora* sp., *Oedogonium* sp., *Rhizoclonium* sp., and *Spirogyra* sp.*)*
Organic Detritus	*autochthonous:* —phytoplankton (esp. *Anabaena* spp.) *allochthonous:* —marginal marsh vegetation [reeds *(Phragmites communis)*, sedges *(Scirpus* spp.*)*, cord grasses *(Spartina cynosuroides*, and probably *S. alterniflora* and *S. patens)*, and cat tails *(Typha domingensis)*] —phytoplankton (from fresh- and salt-water passes) —Mississippi River overflow material	*autochthonous:* —marginal submerged vegetation (vascular plants, filamentous algae, benthic diatoms) —animal matter from various sources *allochthonous:* —some marginal marsh vegetation [water hyssop *(Brammia monnieri)*, galingale *(Cyperus ochraceus)*, spikerush *(Eleocharis* sp.*)*, smartweed *(Polygonum* sp.*)*, and arrowhead *(Sagittaria lancifolia)*] —floating aquatics [alligator weed *(Alternanthera philoxeroides)* and water hyacinth *(Eichhornia crassipes)*] —woody swamp vegetation [tupelo gum *(Nyssa biflora)* and bald cypress *(Taxodium distichum)*] —wind-blown material

tory species characteristic of other areas foraged from time to time in the weedy shallows, however, suggesting an "edge effect" of some magnitude. Prominent among these forms were the ladyfish, Atlantic needlefish, spotted seatrout, silver perch, tidewater silversides, striped mullet, and blue crab, as well as the young of several species and a variety of small cyprinodontid fishes not considered in the present study (see, however, Simpson and Gunter 1956).

Parenthetically, certain species of freshwater turtles (*Pseudemys* sp.) appear to have a peculiar fondness for *Vallisneria* (sometimes called "turtle grass"), and in areas adjacent to several of the north shore streams (*e.g.* Cane Bayou) the bottoms were denuded of such vegetation by transient turtle populations. Similar habits have been pointed out for Florida turtles by Odum (1957).

Zooplankton

The great importance of zooplankton as a source of nutrition for young fishes in fresh, brackish, and salt waters is widely recognized. As noted in Table I, a variety of zooplankton forms were found to be consumed from time to time, but in the Lake Pontchartrain community this critical trophic position is dominated by the calanoid copepod (*Acartia tonsa*) and to a lesser extent by adult schizo-

pods (*Mysidopsis* sp.) and larval penaeid shrimp. As revealed in Table II, significant quantities of zooplankton were found in the diets of fishes belonging to 9 species. This list would unquestionably have been increased several-fold if the young and juvenile stages of all of the important fish species had been studied.

TABLE II. Fish species in which zooplankton was found to make up at least 5% of the food of some stage of the life history. Although schizopods and larval penaeid shrimp are included here as zooplankton, they may at times belong to the microbenthic fauna

Species	Stage and Size Range (mm)	Percentage of Zooplankton in Food
Bay anchovy (*Anchoa mitchilli*).....	juvenile (30-49)	58
	adult (50-74)	43
Atlantic croaker (*Micropogon undulatus*)..	young (50-124)	54
	juvenile (125-325)	12
Sand seatrout (*Cynoscion arenarius*).....	juvenile (40-99)	32
Threadfin shad (*Dorosoma petenense*)....	juvenile (69-103)	29
Blue catfish (*Ictalurus furcatus*).....	juvenile (60-199)	25
Silver perch (*Bairdiella chrysura*).....	adult (70-143)	24
Spotted seatrout (*Cynoscion nebulosus*)...	juvenile (40-99)	20
Yellow bass (*Roccus mississippiensis*)....	adult (130-195)	18
Tidewater silverside (*Menidia beryllina*)..	adult (40-79)	7

The observed food of the zooplankton feeders varied from one species to the next. Quantities of rotifers, such as were taken in surface plankton tows, often appeared in young bay anchovies and threadfin shad. Masses of copepods, often accompanied by some detritus which suggested feeding near the bottom, were frequently encountered in digestive tracts of young blue catfish, silver perch, spots, Atlantic croakers, and some threadfin shad, as well as adult bay anchovies. Several species had taken quantities of young penaeid shrimp. These included young channel catfish, yellow bass, sand seatrout, spotted seatrout, and adult silver perch. In the case of a number of additional species for which the food of the young was not examined, evidence from the literature of the same or related species suggests that these may also feed heavily upon zooplankton. Such fishes include the young of the ladyfish, largescale menhaden, gizzard shad, blue catfish, and probably all of the remaining sciaenid fishes.

Even though the food habits of young fishes were poorly investigated in the present study and even though the habitat relations of many of the presumed zooplankters are not at present well defined, it is quite clear that the zooplankton directly supports a large share of the immature fish in the lake. In fact, the bay anchovy, which is probably the most abundant single fish species of the community, depends largely upon zooplankton throughout much, if not all, of its life history. Most other fish species which rank high in abundance in the estuary also prey heavily upon the zooplankters, at least during early developmental stages.

Since most of the fish species which inhabit the lake during part of their life histories spawn elsewhere, the importance of autochthonous zooplankton populations in maintaining their stocks is also a function of the availability of this food supply to the young and juvenile stages. Some of the species apparently do not arrive in the lake until the zooplankton-feeding stage is largely past. This is notably the case for those forms which spawn in fresh water, but it is also true to some extent for certain of the gulf-spawning fishes. Problems of transportation and salinity barriers must annually prevent hordes of immature fishes from utilizing the abundant food supply of this fertile estuary, but those which do arrive and which are tolerant of the prevailing conditions rely extensively upon zooplankton.

Micro-bottom animals

This category includes primarily those forms which live in intimate association with the bottom. As indicated in Table I, the adults of many small species and the young of several larger ones are included in this group. Among the consumers, most species of fishes and larger invertebrates were found to feed to some extent upon these small benthic organisms, and for many of the lake inhabitants such food constituted the primary source of nutrition. Fishes and larger invertebrate species in which micro-bottom animals made up a significant portion of the food are shown in Table III. Evidence from the literature of the same or related species suggests that the young or adults of certain other lake inhabitants may sometimes prey heavily upon these micro-bottom animals. Such species include the Atlantic stingray, garfishes, ladyfish, yellowbass, largemouth bass, sand seatrout, spotted seatrout, and southern flounder.

Considering the different components of the microbenthic fauna, it was found that foraminifera seldom appeared in the stomachs of most fish species, but in the mud-loving gizzard shad these protozoans made up about ¼ of the food material. The sheepshead was the only species found to consume quantities of sponge, although spicules were frequently encountered in the stomachs and intestines of several bottom-feeding species. Bits of hydroid which often appeared in the stomachs of the crab-eaters suggested the source of their prey. Annelids were negligible as a food item, even in such forms as the Atlantic croaker, spot, and penaeid shrimp which are known to consume large quantities of these worms in other estuaries.

Heavy predation was suffered by the popula-

TABLE III. Fish and invertebrate species in which micro-invertebrates* were found to make up at least 5% of the food of some stage of the life history

Species	Stage and Size Range (mm)	Percentage of Micro-invertebrates* in Food
Spot *(Leiostomus xanthurus)*	juvenile (40-99)	69
	adult (100-203)	63
Tidewater silverside *(Menidia beryllina)*	adult (40-79)	69
Channel catfish *(Ictalurus punctatus)*	juvenile (76-119)	62
Pinfish *(Lagodon rhomboides)*	juvenile (40-99)	57
	adult (100-150)	21
Blue crab *(Callinectes sapidus)*	juv. and ad. (30-197)	52
Hogchoker *(Trinectes maculatus)*	adult (61-74)	50
Gizzard shad *(Dorosoma cepedianum)*	adult (101-278)	48
Freshwater drum *(Aplodinotus grunniens)*	juvenile (211-347)	48
Blue catfish *(Ictalurus furcatus)*	juvenile (60-199)	29
	adult (200-411)	44
Atlantic croaker *(Micropogon undulatus)*	young (10-49)	24
	juvenile (50-124)	21
	adult (125-325)	35
Sea catfish *(Galeichthys felis)*	juvenile (90-169)	26
	adult (170-229)	21
Sheepshead *(Archosargus probatocephalus)*	adult (218-410)	20
River shrimp *(Macrobrachium ohione)*	adult (48-81)	19
Spotted seatrout *(Cynoscion nebulosus)*	juvenile (40-99)	18
White shrimp *(Penaeus setiferus)*	adult (91-142)	17
Bay anchovy *(Anchoa mitchilli)*	juvenile (30-49)	9
	adult (50-74)	10
Silver perch *(Bairdiella chrysura)*	adult (70-143)	9

* Includes inhabitants of benthos and of vegetation.

tions of small rangia clams and mussels, and these mollusks largely supported the intermediate stages of some of the fish and larger invertebrate species. Important consumers of small mollusks included the blue catfish, spot, Atlantic croaker, sheepshead, river shrimp, white shrimp, and blue crab. Ostracods and harpacticoid copepods were prominent in the food of young spots and were occasionally eaten by other species. Isopods, amphipods, and chironomid larvae, occurring on the deeper bottoms and in the shallow weed beds, were consumed by a wide variety of fishes and especially by the catfishes, tidewater silverside, silver perch, spotted seatrout, spot, Atlantic croaker, and pinfish. Most predatory species were found to take in some small crabs, and the heaviest consumption was noted in the case of the catfishes, Atlantic croaker, and blue crabs, themselves.

The present discussion is hampered by the lack of detailed habitat data for most of the small bottom-dwelling invertebrates and by the fact that lines of distinction between micro- and macro-fauna are arbitrary and often difficult to delineate, especially in the cases of the clams and crabs. Despite these limitations the quantitative food record clearly indicates for the microbenthic animals a role of great importance in the overall trophic oconomy of the community. Of chief significance in this regard are the small clams and mussels, together with the isopods, amphipods, small crabs, and chironomid larvae.

Larger invertebrates

Among the larger invertebrates of significance in the diets of the consumer species (Table I), only the rangia clams, mud crabs, and blue crabs are present in the estuary in large numbers throughout the year. The remainder are seasonal in occurrence or of local distribution. Predatory fishes and invertebrates which were found to feed heavily upon the populations of larger invertebrates are given in Table IV. Large rangia clams formed an important part of the diet of only 2 species of fishes, the freshwater drum and the black drum. Both apparently are able to crush and discard the thick-walled shells, retaining only the softer flesh. Such material was difficult to recognize in stomach analyses so the recorded figures are probably minimal for both species of drumfish.

TABLE IV. Fish and invertebrate species in which larger invertebrates were found to make up at least 5% of the food of some stage of the life history

Species	Stage and Size Range (mm)	Percentage of Larger Invertebrates in Food
Black drum *(Pogonias cromis)*	juvenile (116-218)	99
Largemouth bass *(Micropterus salmoides)*	adult (175-209)	97
Spotted gar *(Lepisosteus oculatus)*	adult (405-555)	71
Alligator gar *(Lepisosteus spatula)*	adult (903-1472)	65
Red drum *(Sciaenops ocellata)*	adult (184-625)	63
Freshwater drum *(Aplodinotus grunniens)*	juvenile (211-347)	42
Yellow bass *(Roccus mississippiensis)*	adult (130-195)	34
Sea catfish *(Galeichthys felis)*	juvenile (90-169)	16
	adult (170-229)	34
Silver perch *(Bairdiella chrysura)*	adult (70-143)	29
Sheepshead *(Archosargus probatocephalus)*	adult (218-410)	20
Atlantic croaker *(Micropogon undulatus)*	adult (125-325)	19
Blue crab *(Callinectes sapidus)*	juv. and ad. (30-197)	14
Spotted seatrout *(Cynoscion nebulosus)*	juvenile (40-99)	6
	adult (100-406)	13
Blue catfish *(Ictalurus furcatus)*	juvenile (60-199)	6
	adult (200-411)	13
Ladyfish *(Elops saurus)*	juvenile (161-280)	10
Channel catfish *(Ictalurus punctatus)*	juvenile (76-119)	10
Pinfish *(Lagodon rhomboides)*	juvenile (40-99)	8
	adult (100-150)	10
Southern flounder *(Paralichthys lethostigma)*	adult (113-380)	8
Bull shark *(Carcharhinus leucas)*	adult (780-805)	5
Sand seatrout *(Cynoscion arenarius)*	juvenile (40-99)	5

Grass shrimp, river shrimp, and mud shrimp, being on the whole rather scarce in Lake Pontchartrain, do not serve as important intermediate foods for the predatory species. Surprisingly, even the very numerous and widely distributed penaeid shrimp (which are widely employed for bait in the sport fishery) were poorly utilized by the predators. As previously pointed out (Darnell 1958), these shrimp may be relatively inacessible on the turbid bottom of the lake. Taken as a group, however, the various species of shrimp did constitute a food source of some importance for the silver perch and spotted seatrout, and to

a lesser extent for the bull shark, ladyfish, yellow bass, largemouth bass, and sand seatrout.

Crabs, on the other hand, suffered very heavy predation and were probably utilized as food interchangeably with small fishes by many of the larger carnivores. Adult mud crabs and young and subadult blue crabs were especially important as prey for the spotted gar, alligator gar, sea catfish, blue catfish, yellow bass, freshwater drum, adult Atlantic croaker, black drum, and red drum. The only predator found to consume adult blue crabs was the adult alligator gar which often forages in the shallow flats and marshy creeks where it devours great numbers of the larger crabs. Other species which seem to take in quantities of crabs on occasion include the ladyfish, gafftopsail catfish, largemouth bass, spotted seatrout, and sheepshead.

Among the larger invertebrates comprising the Lake Pontchartrain community, only the crabs may be considered of great importance as food for the larger predators. Shrimp are relatively unavailable, and larger clams, which are very abundant, cannot be handled by the crushing apparatus available to most of the predatory species.

Fishes as a source of food

Special efforts were made to identify the fishes in the stomachs of the predatory species, and 17 different types were recognized (Table I). In addition, a number of the stomachs contained unidentifiable remains of fishes which may or may not have been consumed alive. In many cases the bottom-feeding species had swallowed scales, vertebrae, and eye lenses which obviously had been gleaned from the benthic material. Sixteen predatory species were found to consume significant quantities of fishes, although only about 8 of these appeared to be primarily piscivorous (within the size-groups investigated). These are listed in Table V. Additional analyses would probably demonstrate fish predation by the gafftopsail catfish, channel catfish, and largemouth bass, as well as by a number of the other species.

The ladyfish was encountered only in a longnose gar where identification was questionable. Clupeids were consumed by several types of predators. Young largescale menhaden were identified in the stomachs of the bull shark, longnose gar, and spotted seatrout, and, in addition, many larval and postlarval clupeids were observed in spotted gars, bay anchovies, and spotted seatrout. Most of these young clupeids were undoubtedly largescale menhaden but some may have been threadfin shad.

Undoubtedly because of its small size and general availability, the bay anchovy was subject to heavy predation and furnished food for at least 10

TABLE V. Fish and invertebrate species in which fishes were found to make up at least 5% of the food of some stage of the life history

Species	Stage and Size Range (mm)	Percentage of Fishes in Food
Longnose gar *(Lepisosteus osseus)*	adult (706-1180)	98
Crevalle jack *(Caranx hippos)*	juvenile (79)	98
Bull shark *(Carcharhinus leucas)*	adult (780-805)	95
Southern flounder *(Paralichthys lethostigma)*	adult (113-380)	89
Sand seatrout *(Cynoscion arenarius)*	juvenile (40-99)	54
	adult (100-225)	87
Ladyfish *(Elops saurus)*	juvenile (161-280)	82
Spotted seatrout *(Cynoscion nebulosus)*	juvenile (40-99)	48
	adult (100-406)	79
Atlantic needlefish *(Strongylura marina)*	adult (357-457)	63
Alligator gar *(Lepisosteus spatula)*	adult (903-1472)	35
Yellow bass *(Roccus mississippiensis)*	adult (130-195)	35
Spotted gar *(Lepisosteus oculatus)*	adult (405-555)	24
Silver perch *(Bairdiella chrysura)*	adult (70-143)	24
Blue catfish *(Ictalurus furcatus)*	adult (200-411)	22
Red drum *(Sciaenops ocellata)*	adult (184-625)	17
Atlantic croaker *(Micropogon undulatus)*	juvenile (50-124)	6
	adult (125-325)	14
Pinfish *(Lagodon rhomboides)*	juvenile (40-99)	5

predatory species including the ladyfish, blue catfish, bay anchovy (cannibalism), Atlantic needlefish, crevalle jack, silver perch, sand seatrout, spotted seatrout, Atlantic croaker, and southern flounder. The bay anchovy appeared to be especially important in the diet of the ladyfish, the sand seatrout, and the spotted seatrout, although more intensive analyses of the food of the crevalle jack and the southern flounder might indicate a similarly heavy dependence upon this important forage species. Habitat distributions of the above predators suggest that the anchovy is an important prey species in the weedy shallows as well as in the surface and bottom waters of the open lake.

The sea catfish was found in the stomach of a single longnose gar. The speckled worm eel had been eaten by an adult Atlantic croaker. Pipefish were encountered in blue catfish and an adult Atlantic croaker, both of which seem to feed heavily upon small bottom animals in waters of all depths. Sheepshead minnows which inhabit the marshy lake margins were found in the stomachs of yellow bass and croakers. Sailfin mollies which also inhabit the shallow waters had been eaten only by yellow bass. Striped mullet appeared in bull sharks and alligator gars, and field observations suggested that this predation may sometimes be intense. Tidewater silversides and young seatrout were noted only in blue catfish.

Seven species of predators were found to consume young Atlantic croakers. These included the bull shark, blue catfish, yellow bass, spotted seatrout, Atlantic croaker (cannibalism), sheepshead, and southern flounder. Most of the young croakers were undoubtedly taken near the bottom in deeper

waters, although some may have been consumed in the marginal shallows.

The predator of the adult black drum was not positively identified although, as pointed out earlier (Darnell 1958), the drum was assumed to have been attacked by a bull shark. Small bottom-living naked gobies were consumed by yellow bass, Atlantic croakers, and pinfish. The bay whiff appeared only in a blue catfish.

Fishes were an important source of food for the predators of Lake Pontchartrain. Whereas a variety of fishes were occasionally consumed, intense predation was found to center upon 3 species, the largescale menhaden, bay anchovy, and young Atlantic croaker. Enormous populations of all 3 species are present in the lake, and all are rather widely distributed in shallow as well as deeper waters. The largest predators of the community including the bull shark, the three species of gars, and the jackfish were poorly studied, hence it is impossible to state in detail the nature of their prey. Undoubtedly these forage heavily upon the 3 chief prey species, although the striped mullet also seems to be taken in large numbers. Consumption of cyprinodonts and poeciliids indicates shallow water foraging by a number of the predators.

Terrestrial insects

Terrestrial insects occasionally appeared among the stomach contents of many of the Lake Pontchartrain animals. In most instances they were not abundant and were considered to have been dead when picked up from the water surface or the bottom. Insects, however, made up a more substantial portion of the diet of the Atlantic needlefish and tidewater silverside, both of which feed at the surface and often in the weedy shallows. Terrestrial insects are probably also consumed by the hordes of small cyprinodont fishes and to a lesser extent, by the poeciliids which forage among the marginal marsh vegetation (Darnell 1961, Hiatt 1947a, b, Simpson and Gunter 1956), but the importance of this food source for the lake residents in general is obviously very small.

Organic detritus and bacteria

Organic detritus is understood here to include all types of biogenic material in various stages of bacterial decomposition. As indicated in Table I, the vegetable detritus of Lake Pontchartrain seems to be derived primarily from the decay of certain marsh grasses and phytoplankters. Detritus of animal origin includes chiefly the remains of zooplankton and microbenthic animals and less frequently the bodies of larger crustaceans, fishes, and terrestrial insects. Other autochthonous and allochthonous sources of organic detritus will be discussed subsequently. These decaying materials are often associated with large masses of bacteria which have a rather characteristic appearance.

From the beginning of the study an effort was made to distinguish between organic detritus and larger masses of tissue which, although of obscure origin, were clearly more homogeneous. Such "undetermined organic matter" may have been dead and slightly decayed when consumed or alive and subsequently digested beyond recognition. No general criteria for distinguishing between these alternatives were developed so undetermined organic matter may sometimes have been confused with organic detritus and *vice versa*.

Clearly, the detritus was often consumed as a heterogeneous mixture and its source could often be deduced from the admixed materials, especially hard parts. Since the aquatic animals can digest neither cellulose nor chitin the appearance of these substances often provided critical clues. Other such materials included frustules of benthic and planktonic diatoms, sponge spicules, hydroid stems, shells (of foraminifera, snails, and clams), fish bones and eye lenses, and particles of sand and silt.

Among the larger consumers nearly all had ingested some material classified as organic detritus, and in 25 species of fishes and invertebrates this material was considered to have made up at least 5% of the ingested food (see Table VI). Certain "iliophages" such as the striped mullet and the gizzard shad and certain "omnivores" such as the various catfishes, invertebrates, and smaller sciaenids might have been expected to take in some organic detritus. The predominance of this material in the food of some stage of over ¼ of the species examined, however, and its utilization in significant quantities by even the most carnivorous species clearly points to the great importance of organic detritus in the food of all "classes" of consumers in this estuarine community.

Several species appeared to have obtained detritus by filtration of particulate suspended matter from the water. These included the menhaden, threadfin shad, and the young plankton-straining bay anchovies and young sciaenids. Fine particulate detritus was procured from shallow silty bottoms by the gizzard shad and striped mullet. Several different types of detritus were encountered in the digestive tracts of the bottom-feeding catfishes, sciaenids, hogchokers, clams, shrimp, and crabs reflecting the diverse feeding mechanisms and suggesting a variety of feeding sites in both deeper and shallower waters. The yellow bass and pinfish seem to have fed strictly in the marginal shallows.

Ontogenetic changes in the utilization of detritus were apparent for several species (for details see Darnell 1958). In the case of the blue catfish,

TABLE VI. Fish and invertebrate species in which organic detritus* was found to make up at least 5% of the food of some stage of the life history

Species	Stage and Size Range (mm)	Percentage of Organic Detritus* in Food
Largescale menhaden *(Brevoortia patronus)*	young (38-48)	11
	juvenile (85-103)	99
Striped mullet *(Mugil cephalus)*	juv. and ad. (97-327)	79
Common rangia *(Rangia cuneata)*	adult (35-38)	73
Atlantic croaker *(Micropogon undulatus)*	young (10-49)	22
	juvenile (50-124)	57
	adult (125-325)	31
White shrimp *(Penaeus setiferus)*	adult (91-142)	58
Sea catfish *(Galeichthys felis)*	juvenile (90-169)	56
	adult (170-229)	44
River shrimp *(Macrobrachium ohione)*	adult (48-81)	55
Gizzard shad *(Dorosoma cepedianum)*	adult (101-278)	50
Hogchoker *(Trinectes maculatus)*	adult (61-74)	50
Blue catfish *(Ictalurus furcatus)*	juvenile (60-199)	36
	adult (200-411)	8
Bay anchovy *(Anchoa mitchilli)*	juvenile (30-49)	33
	adult (50-74)	34
Spot *(Leiostomus xanthurus)*	juvenile (40-99)	29
	adult (100-203)	34
Atlantic needlefish *(Strongylura marina)*	adult (357-457)	32
Channel catfish *(Ictalurus punctatus)*	juvenile (76-119)	28
Blue crab *(Callinectes sapidus)*	juv. and ad. (30-197)	26
Pinfish *(Lagodon rhomboides)*	juvenile (40-99)	16
	adult (100-150)	20
Threadfin shad *(Dorosoma petenense)*	juvenile (69-103)	15
Red drum *(Sciaenops ocellata)*	adult (184-625)	15
Tidewater silverside *(Menidia beryllina)*	adult (40-79)	14
Silver perch *(Bairdiella chrysura)*	adult (70-143)	14
Yellow bass *(Roccus mississippiensis)*	adult (130-195)	11
Freshwater drum *(Aplodinotus grunniens)*	juvenile (211-347)	10
Sand seatrout *(Cynoscion arenarius)*	juvenile (40-99)	9
	adult (100-225)	8
Ladyfish *(Elops saurus)*	juvenile (161-280)	8
Spotted seatrout *(Cynoscion nebulosus)*	juvenile (40-99)	8
	adult (100-406)	8

* Some non-detritic organic matter may also be included. See text.

increase in size was accompanied by a marked reduction in the relative intake of this material, and the same was true to less extent for the bay anchovy, tidewater silverside, sand seatrout, and spotted seatrout. All of these forms tend to become progressively more carnivorous and more selective with increase in size. In the case of the spot the reverse was true. Large spots ingested relatively greater amounts of detritus than did small spots, a fact correlated with the progressive increase in utilization of small bottom animals. In the Atlantic croaker the greatest consumption of detritus occurred in the middle sizes, and this general pattern also appeared in the pinfish.

These studies point to the major contribution of organic detritus to the total food volume of the fishes and larger invertebrates of the Lake Pontchartrain community. Detritus is available as fine suspended particles and as precipitated benthic material, and both forms appear to be widely used. The nutritive value of the detritus or its associated bacteria have not been investigated in the present study. ZoBell and Feltham (1938, 1942) pointed out, however, that the bacteria associated with a given particle of detritus often constitute a large percentage of the volume of the substrate itself. These workers have also noted that a variety of aquatic invertebrates and some vertebrates can live almost indefinitely upon a diet composed largely or exclusively of bacteria. Available evidence, although somewhat indirect, strongly suggests for the organic detritus a very significant role in the nutritive relations of the Lake Pontchartrain community. The detritus problem will be discussed in greater detail elsewhere.

NUTRITION OF SMALLER CONSUMERS

Food of the zooplankters

The relative importance of the various sources of primary organic matter in terms of total zooplankton production may be inferred from the pattern of distribution of zooplankton volumes within the lake based upon surface samples. In Figure 1 each number represents the overall average of the zooplankton volumes (expressed as cc per cubic meter of water) observed at the particular monthly collecting station. The greatest average volume was observed near the salt water entrance (3.0). Areas strongly affected by the inflowing current of salt water gave fairly high average values which decreased with the distance from the salt-water pass (0.67, 0.48, 0.44). A high value was also observed near the entrance of the fresh-water pass (0.66). Near one of the south-shore areas of intense wave erosion zooplankton was abundant (0.77), and the volume decreased somewhat with distance from this shore (0.53). Lowest zooplankton volumes were observed in relatively infertile areas beyond the influence of the passes and the eroding shores. Stations yielding low average values were located near the center of the lake (0.31), in the vicinity of protected sandy shores (0.32, 0.26), and off-shore from the New Orleans seawall (0.19). Clearly, the areas of greatest surface zooplankton abundance are those characterized by mixing of water masses, bottom roiling, and proximity to eroding marshes.

Attempts to determine the food of the most abundant copepod, *Acartia tonsa,* met with only partial success. Dissection of a series of preserved specimens provided no definite results because of the difficulty of dissection and the possibility of adherent material being confused for food. Twelve specimens cleared in beechwood creosote and mounted in balsam revealed 2 which definitely contained a few small diatoms (*Melosira* sp.) and 2 others which may have contained broken diatom parts. The digestive tracts of all specimens, however, included a quantity of dark unidentifiable material, sometimes granular in appearance, which

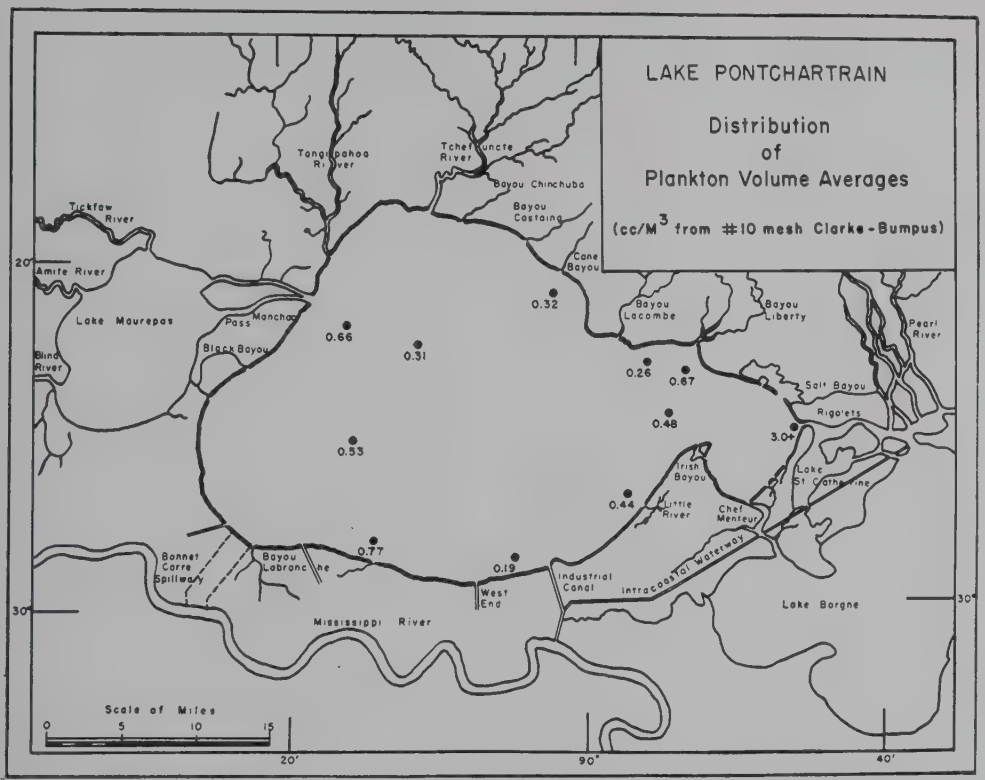

FIG. 1. Average plankton volumes for monthly collecting stations within Lake Pontchartrain. Since the figures are based entirely upon collections made with the Clarke-Bumpus tow net (with number 10 mesh net), they are interpreted as representing primarily zooplankton volumes. The extreme figure observe at the Rigolets, however, represents, in part, enormous blooms of diatoms (*Coscinodiscus* and others).

appeared to be bits of organic detritus. Connover (1956) successfully reared *A. tonsa* in the laboratory on diatom cultures, and he found that specimens taken in Long Island Sound frequently contained whole small diatoms and fragments of larger ones. He noted further that guts of field collected specimens always contained a considerable quantity of "greenish material of unknown origin." In Lake Pontchartrain this large copepod undoubtedly consumes the abundant diatoms to some extent, but it also appears to make considerable use of suspended organic detritus. The smaller zooplankters probably depend upon detritus and smaller phytoplankters, but direct evidence is lacking. The zooplankton volume studies suggest that detritus from the passes, bottoms, and marshy shores is an important factor in support of the zooplankton populations.

Food of the micro-bottom animals

Food of the microbenthic animals was not investigated in the present study. These forms may be assumed to rely heavily upon detritus and associated bacteria on the basis of the following considerations: knowledge of their food habits in other estuaries, importance of detritus in the diets of the larger mobile species, and the availability of organic detritus on the bottom of Lake Pontchartrain. As revealed in Petersen dredge samples taken throughout the lake, the bottom surface consists of a thin ooze, brown to blue-green in color, which is probably made up largely of precipitated and decaying *Anabaena* cells mixed with detritus from other sources.

SOURCES OF PRIMARY ORGANIC MATTER

In the present study no attempt was made to measure primary production. From the standpoint of community nutrition, however, it may be pointed out that secondary production within the estuary depends to a considerable extent upon organic material originating elsewhere. Briefly, the important sources of organic material may be outlined as follows:

A. *AUTOCHTHONOUS*
1. Phytoplankton
2. Marginal submerged vegetation (vascular plants, filamentous algae, and benthic diatoms)
3. Bacteria

B. *ALLOCHTHONOUS*
1. Marginal marsh vegetation
2. Phytoplankton (from fresh- and salt-water passes)
3. Mississippi River overflow material
4. Woody swamp vegetation
5. Wind-blown material.

In the following discussion these topics are treated individually in order to clarify the relative importance of each basic food source and to expose some of the factors involved in their utilization.

Phytoplankton

Estimates of the standing crop of phytoplankton and zooplankton are available for a 15-month period from Februray, 1954 through May, 1955. The phytoplankton estimates are based upon counts of centrifuged water samples, whereas the zooplankton estimates are based upon counts from Clarke-Bumpus tow net samples (using #10 mesh nets). Each of the above methods is open to certain criticisms, and, although the 2 methods do not yield exactly comparable results, the data may be used for order-of-magnitude comparisons. Trends in the monthly averages of the phytoplankton and the zooplankton populations based upon surface samples are given in Figure 2. These data indicate that during most of the year the standing phytoplankton populations were numerically lower than the standing zooplankton populations. Such conditions have been reported by other authors (Edmondson 1957, Davis 1958). In certain reported instances the relative scarcity of phytoplankters seems to have been due to the grazing activities of the zooplankters, but in the present case it may be attributed, in part at least, to the heavy load of suspended detritus and silt, decreasing light penetration and, hence, photosynthetic activity.

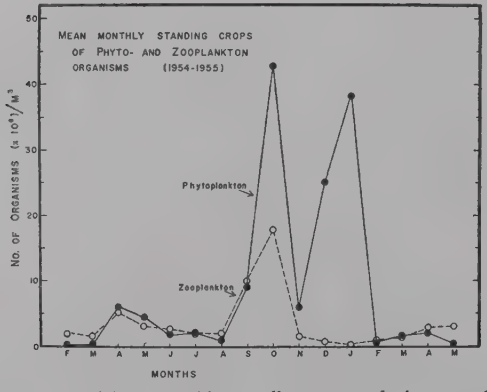
MEAN MONTHLY STANDING CROPS
OF PHYTO- AND ZOOPLANKTON
ORGANISMS (1954-1955)
No. OF ORGANISMS (x 10³)/M³
Phytoplankton
Zooplankton
F M A M J J A S O N D J F M A M
MONTHS

FIG. 2. Mean monthly standing crops of phyto- and zooplankton organisms of Lake Pontchartrain (February, 1954 through May, 1955). Note the close correspondence of phytoplankton and zooplankton levels during most of the months.

The most consistently abundant phytoplankton organisms in Lake Pontchartrain, large thick-shelled diatoms of the genera *Chaetoceros* and *Coscinodiscus,* were undoubtedly utilized to some extent by the large copepod, *Acartia tonsa,* but they must have been of little value for the smaller rotifers and protozoans. These diatoms were seldom encountered in the stomachs of the fishes examined. Armored dinoflagellates which were seasonally abundant must also have been a poor food source for most small consumers. Whereas smaller flagellates and other phytoplankters may have contributed more significantly in this respect, there is no direct evidence either for the abundance of such forms or for their extensive utilization as food.

Probably the most important phytoplankton organisms from the standpoint of community nutrition were the surface-floating blue-greens (especially *Anabaena* spp. and, to a lesser extent, *Microcystis* spp.). These forms, although seasonal in occurrence, were sometimes extremely abundant and were found to be utilized readily by some of the fishes. Food of the larvae and very young of most types of fishes was not studied, and phytoplankton may have been of direct importance for species with pelagic larvae, especially the clupeids, engraulids, and atherinids.

Perhaps the real significance of the phytoplankton populations of Lake Pontchartrain lies in their contribution to the general fund of organic detritus within the lake. In this connection it may be noted that minute spherical bodies probably derived from disintegrated colonies of *Anabaena* or *Microcystis* made up about 1/6 of the observed food volume of the clam, *Rangia cuneata,* the most important bottom invertebrate in the lake. Such bodies were also encountered in the digestive tracts of the river shrimp, *Macrobrachium ohione.* Diatoms, although never abundant, did appear in the digestive tracts of several species of bottom-feeding fishes and invertebrates. In view of the tremendous seasonal abundance of certain phytoplankton species and the general shallowness of the lake, allowing recirculation of precipitated materials, the autochthonous phytoplankton populations must constitute one of the major sources of organic nutrients for the consumers. The extent to which the consumers rely upon this material as an ultimate source appears to be considerable even if the importance cannot be assessed quantitatively on the basis of existing knowledge.

Marginal submerged vegetation

A series of transects from deep water to shore in numerous likely areas around the margin of the lake revealed no rooted vegetation growing in water deeper than 6 feet, as might be expected in view of the high turbidity. Limited beds of *Vallisneria spiralis* and *Ruppia maritima* were found along the north shore and in spots along the east and southeast shores, but such beds were not extensive and were limited largely to shallow sandy bottoms in protected areas. Species of *Jussiaea* and other genera were found locally in fresher areas of the northwest shore. Most of the filamentous green algae (including species of *Cladophora, Oedogonium, Rhizoclonium,* and *Spirogyra*) were encountered growing in beds of larger vegetation, although broken mats of such algae were sometimes collected from deeper areas, having been transported by water currents.

Many species of small invertebrates including amphipods, isopods, and palaemonid shrimp inhabit the shallow-water weed beds, and some of these undoubtedly feed directly upon the rooted vegetation, the filamentous algae, or the accompanying epiphytes. Food relations of the small invertebrate inhabitants of the weedy shallows were not studied. Since these beds are not extensive, such relations probably play only a minor role in the total economy of the lake community. If the marginal weeds had been more extensive (as they apparently were in the historical past before man began filling in the shallow areas of the south shore and attempting to stabilize the lake margins), the invertebrate and fish populations inhabiting the lake, no doubt, would have been quantitatively different with a relative numerical increase in species which frequently or consistently are nourished by the marginal vegetation or its inhabitants.

During stomach analyses, bits of *Vallisneria, Ruppia,* and filamentous green algae in various stages of decay were sometimes identifiable. These do not seem to have contributed much to the total fund of organic detritus of the lake and must be considered, at best, a very minor source of organic matter in Lake Pontchartrain.

Benthic diatoms have been suggested as an important source of nutrition in the Danish Waddensea by Smidt (1951). These may also prove to be of local importance in some of the marginal areas of Lake Pontchartrain, especially in the northwestern and southwestern sectors. Schools of striped mullet were occasionally observed feeding upon the bare mud surface in a shallow marginal lagoon in the vicinity of Bayou La Branche near the southwest corner of the lake, and bottom diatoms and other surface algae must have been the major attractions. The relative scarcity of such shallow-water mud and sand flats, however, would seem to preclude benthic diatoms as a major source of organic matter for the lake as a whole.

Bacteria

Bacteria have not been investigated in the present study. In natural waters, in general, they may include both autotrophic and heterotrophic species. Although most autotrophic bacteria require rather specialized habitats, some may be present in the lake, and, if photosynthetic, they would be trophically similar to the phytoplankton. The heterotrophic species include those which subsist principally upon dissolved or adsorbed nutrients as well as the decomposers which derive nourishment from particulate organic matter. Decomposers undoubtedly make up the bulk of the bacteria in the lake, and, as noted earlier, enormous numbers must be ingested by the fish and invertebrate consumers in connection with the detritus.

Marsh vegetation

Of considerable importance in the metabolism of the total community is the contribution of marginal marsh vegetation, and it is quite conceivable that a greater quantity of the organic material in the bottom of Lake Pontchartrain is derived from this source than from all other sources combined. The chief contributing species seem to be the emergent hydrophytes and low flood-plain plants including reeds (*Phragmites communis*), sedges (*Scirpus* spp.), cord grasses (*Spartina cynosuroides* and probably *S. alterniflora* and *S. patens*), and cat tails (*Typha domingensis*). Of less probable importance are water hyssop (*Bramnia monnieri*), galingale (*Cyperus ochraceus*), spikerush (*Eleocharis* sp.), smartweed (*Polygonum* sp.), arrowhead (*Sagittaria lancifolia*), and the floating aquatics, alligator weed (*Alternanthera philoxeroides*), and water hyacinth (*Eichhornia crassipes*), all of which have been identified from the shores of Lake Pontchartrain in the present study. These and other species comprise extensive marshes, especially along the northern, southern, and eastern margins of the lake (for details see Penfound and Hathaway 1938). Such shores are subject to heavy erosion by wave action caused primarily by hurricanes and other strong winds. Steinmeyer (1939) pointed out that both the north and south shores are receding under the influence of erosion and that the rate of recession in some areas is remarkably rapid. He noted for one marsh shoreline in the eastern sector of the lake an average rate of regression of about 14 ft per year over the 50-year period of the comparison.

During the field work the seine crews encountered great difficulty in areas of intense erosion because of the irregular bottoms. When the winds were really high (over 25 mph) no field work was attempted. At times of moderate wind and wave action the shore water was found to be quite turbid because of the suspension of chopped and decaying marsh grasses ("coffee grounds" in local terminology). Secchi disc visibility readings of one inch and less were then recorded. Shallow turbid waters adjacent to such eroding shores are teeming centers of biological activity and constitute areas of great concentration of numerous species. On one occasion at the Kenner Towers station on the south shore the 150 ft (¾ inch mesh) beach seine was dragged ashore by an experienced crew only by extreme effort. The contents of the seine included literally tons of this organic material mixed with bushels of penaeid shrimp, blue crabs, Atlantic croakers, sea catfish, largescale menhaden, some striped mullets, and a bull shark. All of these species are frequently found in such environments, and probably all except the shark were consuming the decaying humus, either from the bottom or by filtration from the water. In only a few of the stomachs analyzed, however, was the organic material certainly of this nature. More frequently the state of decomposition precluded exact determination of the source.

Petersen and Jensen (1911) in Denmark early noted, "It is thus characteristic of the metabolism of the sea that the organic materials do not remain at the place where they were produced, but are distributed more or less uniformly over large areas." In Lake Pontchartrain, also, the products of marsh erosion are picked up by currents, and the finer particles, at least, are transported throughout the lake. This was indicated by the distribution of turbid water following periods of high winds. Steinmeyer (1939) found the organic content of bottom sediments to be highest in the deepest basins, further pointing to offshore transport. The great importance of this detritus in supporting secondary production will be discussed in a later section.

Other sources of organic matter

Several additional sources of organic matter are available to the community, and some may be of great overall significance. Since their importance can be inferred only in a general way at the present time, these will simply be mentioned here for the sake of completeness. The first source is the allochthonous plankton and other suspended matter which enters the lake through the fresh- and saltwater passes. Much of the inflowing suspended material is precipitated near the entrances to the estuary forming broad subaquaeous bars. Such areas are highly productive of fishes and invertebrates and must be considered centers of great biological activity. As indicated by the plankton samples, however, some of the inflowing material may also be transported widely within the lake.

Another source of organic material is the Mississippi River. Previous to the formation of artificial levees the river naturally overflowed into Lake Pontchartrain through great "crevasses." Steinmeyer (1939) reported that in one such overflow at least a third of the flood stage volume of the river was flowing through the lake. More recently, following the construction of artificial levees and the Bonnet Carré Spillway, the floodwaters are allowed to enter the lake only in times of exceptionally high water. Most of the material contributed by the river at such times undoubtedly consists of inorganic silt such as that comprising the bottom throughout the shallow southwestern sector of the lake today, although some organic material also is added. Whereas the immediate effect of the spillway opening upon the Lake Pontchartrain populations is probably to drive out the motile and destroy many nonmotile forms through the combined actions of heavy silt and much fresh water, there is some reason to believe that there may be a long term enhancement of production by the addition and redistribution of nutrients (see Butler 1952, Butler and Engle 1950, Gowanloch 1950, Gunter 1953, Owen and Walters 1950, and Viosca 1938).

The western sector of the lake is bounded largely by swamps dominated by bald cypress (*Taxodium distichum*) and tupelo gum (*Nyssa biflora*) and containing other woody species. As a result of former Mississippi River overflow and hurricane action much woody material derived from this source has been deposited in the lake bottom, and this is especially concentrated in the vicinity of Black Bayou on the extreme western shore. Probably the effect upon the lake as a whole is negligible, but locally this material is of some importance. Wind-brown material such as pollen, probably contributes relatively little to the general fund of organic matter in the lake.

Evidence cited above supports the conclusion that the basic organic matter supporting the consumers in the Lake Pontchartrain community is partly, if not largely, allochthonous. Direct consumption of phytoplankton or marginal vegetation appears to be low, and much of the vegetable matter which enters the consumer portions of the community apparently does so through the medium of detritus following death and decay, transport and precipitation. This vegetable detritus has a very complex origin.

Discussion

Lake Pontchartrain is not a microcosm, but a broadly open system. As noted previously, the basin is rapidly filling due to the accumulation of materials from a variety of sources. Much of this material originates outside the lake and enters in the form of humus from marginal wave-dissected marshes or as plankton from the adjacent fresh- and salt-water areas. Within the lake such material undergoes bacterial decomposition, and as detritus it is ingested by many copepods, bottom invertebrates, and fishes. From the standpoint of nutrition, therefore, many of the most important consumer species of the Lake Pontchartrain community seem to depend largely upon primary production of areas outside the lake.

From field survey data it is quite clear that most of the larger consumer species which forage in the lake are not year-around residents, but are transients which spend only a fraction of their lives there. These include many species of fishes and larger invertebrates whose young migrate in from the Gulf and make use of the estuary as feeding grounds, especially during the warm summer months. Likewise, a number of consumer species enter from the fresher areas, primarily during winter. From the trophic standpoint, therefore, the community draws heavily upon surrounding areas, not only for nutrients, but also for consumers. Certain practical consequences of this are being considered elsewhere.

Detritus of vegetable origin seems to be the most important single food material ingested by the fish and invertebrate consumers. Thus, bacteria constitute an intermediate step (or series of steps) between primary production on the one hand and animal nutrition on the other. Heterotrophic bacteria must then be considered the chief "primary consumers" within this estuarine community.

Overall nutrient relations in natural communities were depicted by many early workers in terms of classical "food chain" and "food web" diagrams. Although such diagrams do give much insight into community interactions, they do not provide an adequate basis for quantitative consideration of the nutritional pathways among the consumer species. Another approach, which involves the concept of "trophic levels," has been employed by Lindeman (1942) and a number of subsequent workers.

Noting that efficiency of energy transfer in biological systems seldom exceeds a few percent, these authors have pointed out that the effective number of major energy transfers within the ecosystem is usually limited to 3 or 4. Thus, a given quantity of energy fixed by the green plants is almost completely dissipated after passage through 3 or 4 consumer species. In a simple hypothetical ecosystem where only one species consumes plants, another consumes the plant-eaters, and another consumes the plant-eater predators, it may be said that the herbivore is a "primary consumer," the plant-eater is a "secondary consumer," and the species which consumes the plant-eater is a "tertiary consumer." As pointed out by Ivlev (1945), Odum (1959), and others, however, it cannot be assumed that in natural communities given species will conform to specific trophic levels. Unfortunately, in the absence of food studies providing evidence to the contrary, a number of writers have ignored this important point.

Data from the Lake Pontchartrain study indicate that most of the consumer species do not conform to specific trophic levels. The evidence may be summarized as follows:

1. Animals of a given size group of a particular species often consume significant amounts of material from several different sources. It would be highly misleading to assign adult blue catfish, Atlantic croaker, and sheepshead (among others) to such specific trophic levels. The food of the adult blue catfish included mollusks (12%), macrocrustacea (17%), fishes (30%), vegetation (26%) and miscellaneous material (15%). Food of the adult Atlantic croaker included mollusks (40%), crabs and shrimp (24%), fishes (22%), and miscellaneous material (14%). Food of the adult sheepshead included mollusks (28%), vegetation (54%), and miscellaneous material (18%). The same phenomenon would apply, with slightly less emphasis, to most of the larger consumer species.

2. Alternative foods may be utilized from time to time and from place to place depending upon availability. Such food substitutions clearly do not take place within the confines of a given "trophic level." A considerable body of evidence has now accumulated indicating that many of the most successful species of fishes and invertebrates are opportunists and that, within the range of what they can apprehend, manipulate, and ingest, their food habits are governed to a great extent by what is easily available. This is well illustrated by the fact that many of the consumer species will eat their own young when the opportunity arises. The geographic and environmental variation in food habits of the channel catfish, striped mullet, freshwater drum, spotted seatrout, and Atlantic croaker which have been noted previously (Darnell 1958) provide further evidence of opportunism among the consumers.

3. The ontogenetic progression of food habits within a given species frequently involves successive specialization upon widely different types of foods. This is most striking in the case of the fishes. In the spotted seatrout the food progression seems to involve (in some cases) the change from zooplankton to larger crustaceans to fishes. In the Atlantic croaker the shift proceeds from zooplankton to small bottom animals to detritus to larger crustaceans and fishes. In the pinfish the ontogenetic change involves small crustaceans, followed by detritus, then vegetation. Many other examples could be given.

4. In Lake Pontchartrain most of the consumer species ingest large quantities of organic detritus, and some seem to be largely dependent upon this material. As pointed out above and is discussed by Gneri and Angelescu (1951), organic detritus has a very complex origin, includes much bacteria, and involves varying quantities of recirculating animal protoplasm.

Evidently (as suggested by Petersen and Jensen, 1911) the consumers exhibit a broad disregard for narrow trophic lines. In fact, the ability of a given species to utilize alternate foods (often from different "trophic levels") appears to be one of the main buffering factors which tend to stabilize population levels in complex natural communities. To ignore the inherent diversity and the system of alternatives would seem to be overlooking the very essence of trophic integration involved in community balance. Actually, Lindeman (1942) cautioned that the higher trophic levels are not as distinctly recognizable as the lower levels, and in the present estuarine community, at least, they do not seem to be recognizable at all.

In the presentation of food analysis data it is highly desirable to provide a record which is both quantitative and comparative. An approach to such a system has been found in the "trophic spectrum" (see Figure 3). In this method the food categories, as determined by the investigator, are listed along the left in sections of equal height and are arranged in approximate order of concentration of the food (from detritus through vegetation and invertebrates to vertebrates). On the right, for a given size class of fish, there are placed horizontal bands whose height corresponds to the percent volume of food observed in the particular food category. The sum of the heights of all the bands within a given spectrum equals 100%, which is also the standard height of each food category. On this basis the food spectra for several size classes of one fish species can be compared quantitatively at a glance.

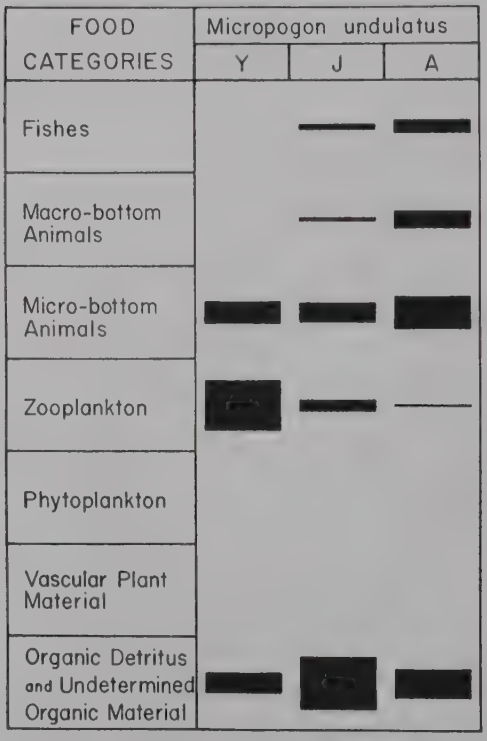

Fig. 3. Trophic spectra for young, juvenile, and adult stages of the Atlantic croaker (*Micropogon undulatus*) from Lake Pontchartrain. Note the shift in emphasis from zooplankton in the young through detritus in the juvenile to bottom animals and fishes in the adult.

The same method may be utilized to compare several species or to represent a community. In Figure 4 the available food spectra for the consumers of the Lake Pontchartrain community are presented. Ignoring details, the following points of overall community importance may be seen:

1. Phytoplankton and vascular plant material are utilized directly by only a few of the consumer species.
2. Organic detritus (including some organic matter of undetermined origin) was encountered to some extent in almost all consumer groups, and this material was found to be used more consistently than any other food category. Most of the abundant species of the community rely heavily upon this material at some stage of their life histories.
3. Zooplankton is ingested primarily by immature stages of the consumers. (If the young stages of more consumer species had been examined, this food category would, doubtless, have been greatly enlarged).
4. Small and large bottom animals and fishes were taken in great quantity by a variety of species. Some of the consumers tended to specialize upon forms within a particular food category, but many fed simultaneously from several different categories.
5. No sharp dividing lines exist between consumers of different food categories.

In conclusion it is noted that the really abundant fish and invertebrate species of the Lake Pontchartrain community belong to either of 2 groups. The first includes those forms which feed largely upon organic detritus. These are represented by the rangia clam, striped mullet, largescale menhaden, white shrimp, and hogchoker. The 2nd group includes those species which have a rather wide range of food tolerance and are omnivores in the broadest sense. These are represented by the sea catfish, bay anchovy, spot, Atlantic croaker, and blue crab. Around these forms the rest of the community revolves.

Summary

1. The Lake Pontchartrain community is a broadly open system exchanging nutrients, producers, and consumers with adjacent fresh-water and salt-water areas as well as with neighboring marshes and swamps.
2. Consumers within the lake apparently depend in great measure upon primary production which

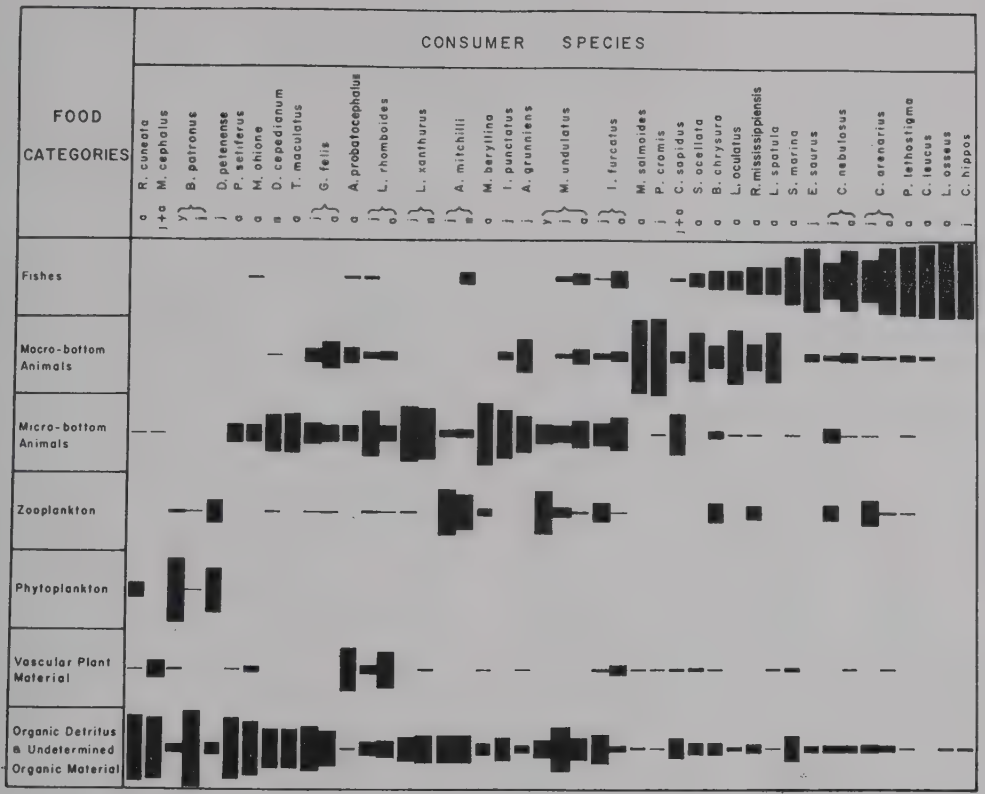

FIG. 4. Trophic spectra for the most important consumer species of the Lake Pontchartrain community. Note relatively little utilization of phytoplankton, vascular plant material, or zooplankton, but heavy emphasis upon detritus, bottom animals, and fishes.

takes place outside the lake. Hence, the estuarine community may be trophically unbalanced.

3. The most conspicuous single food item in the diets of the consumers of this community is organic detritus with its attendant bacteria.
4. Individual species do not appear to conform to specific trophic levels on the basis of the following considerations:
   a. Omnivory on the part of most, if not all, of the major consumer species,
   b. Nutritional opportunism among the consumers,
   c. Ontogenetic change in the food habits of the consumers,
   d. Importance of organic detritus in the nutrition of the consumer species,
   e. Complex nature of the origin of detritus.
5. An alternative model of the trophic reltions of the community is presented which represents the observed food of each species in the form of a spectrum and in which each type of food can be represented quantitatively and comparatively.
6. The really abundant consumer species of the Lake Pontchartrain community comprise 2 groups: those which feed heavily upon organic detritus and those which exhibit a broad range of food tolerance.

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REPORTS

BOTANICAL NOTES ON THE CANARY ISLANDS. III. THE LIFE FORM SPECTRUM AND ITS INTERPRETATION

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THE FLORA

A recent compilation of the flora of the Canary Islands (Lems 1960b) makes it possible to calculate biological spectra for each of the islands. The total flora of vascular plants is estimated at 1531 species (new discoveries of endemic rarities and new immigrant weeds will keep changing this number). There are 440 endemic Canarian species, 251 of which are known from a single island only. Another 104 species are Macaronesian, i.e. shared with other islands in the North Atlantic and the adjacent shores of Africa. The remaining 987 species are immigrants from the Mediterranean, from tropical Africa and America; at least 137 of these arrived with Man as ornamentals and crop plants, but probably many more depended on Man as camp followers. It is impossible to say just which species are native, which introduced, because long before the conquest of the Canary Islands by Europeans in the 14th century, a prehistoric tribe of men (the Guanches) had reached the archipelago (Bannerman 1922). No doubt they brought with them plants whose descendants are now thoroughly naturalized.

LIFE FORMS

The life form classification devised by Raunkiaer (1934) is here applied to the plants of the Canary Islands. (A marginal punch card was made for each species. Such criteria as life form, dispersal type, leaf size, insular distribution, geographic status, and taxonomic affinity were punched out on these).
The major life forms are:

M— trees (macrophanerophytes), not further subdivided because only 62 species are recorded (e.g. *Laurus canariensis, Pinus canariensis, Dracaena draco*).

N— shrubs (nanophanerophytes), a major category with 234 species (e.g. *Euphorbia regis-jubae, Spartocytisus nubigenus, Limonium arborescens, Echium giganteum, Sonchus arboreus*).

Ch—chamaephytes, with buds within 0.3 m above ground level, also a large group, with 246 species (e.g. *Polycarpaea teneriffae, Aeonium canariense, Plantago arborescens*).

H— hemicryptophytes, with buds at soil level, numbering 261 species (e.g. *Carex canariensis, Dactylis smithii, Senecio cruentus*).

Th—therophytes, either annual or biennial and lacking true vegetative renewal buds, the largest group in the flora with 555 species (e.g. *Aichryson punctatum, Resedella subulata, Drusa oppositifolia*).

G— geophytes, with underground buds, 71 species (e.g. *Dracunculus canariensis*).

Hy—hydrophytes, of which only 18 species are recorded (e.g. *Callitriche stagnalis, Zostera nana, Lemna minor*).

Li— lianas, an equally small group of 18 species (e.g. *Convolvulus canariensis, Periploca laevigata, Smilax canariensis*).

E— epiphytes, none of them obligate in the Canaries; only 3 vascular plants (*Davallia canariensis, Polypodium serratum, Vandenboschia radicans*).

SS—stem succulents, with 17 species (e.g. *Euphorbia canariensis, Ceropegia dichotoma, Opuntia ficus-indica*).

All but 46 species could be assigned to one of these life forms. Not enough is known about the 46 to decide where they belong. It must be said also that many of the peculiar plant forms of the Canary Islands do not fit unequivocally in the Raunkiaer scheme. Even field experience, dead and living specimens, often did not ease the task. Long-lived monocarpic plants (*Echium simplex, Aeonium nobile*) pose a problem, being neither annual nor biennial, nor having true renewal buds. Many chamaephytes, wedged between rocks, may double as hemicryptophytes. In spite of these and other difficulties encountered in any artificial classification, the results and correlations made possible by the Raunkiaer system speak for its objective value as a plant geographic tool.

THE BIOLOGICAL SPECTRUM

The significance of life form spectra as indicators of environmental conditions has been the subject of several treatises (Raunkiaer 1934, Cain 1950, Cain & Castro 1959). Greig-Smith (1957) has pointed out the necessity of testing the statistical significance of differences between spectra. Especially significant are those spectra which are based upon complete floristic inventories of natural areas, rather than single habitats or heterogeneous countries.

Table I shows the life form spectra of the Canarian

TABLE I. Life form spectra of the Canary Islands.

	No. spp.	% trees	% shrb.	% cham.	% hemic.	% thero.	% geo.	% hydro.	% lian.	% epi.	% s.s.	% ?
Entire archipelago	1531	4.0	15.3	16.1	17.0	36.3	4.6	1.2	1.2	.2	1.1	3.0
Lanzarote	366	3.0	10.1	14.8	11.7	51.5	5.5	.6	.3	—	.3	2.2
Fuerteventura	348	3.7	12.1	14.7	12.4	47.3	5.2	.6	.3	.3	1.1	2.3
Gran Canaria	763	4.2	14.6	14.9	16.1	40.2	5.1	1.3	1.0	.4	.8	1.4
Tenerife	1079	5.0	14.0	14.7	18.3	37.5	5.1	1.0	1.3	.3	1.0	1.8
Gomera	539	6.1	15.4	16.7	18.4	36.1	3.5	.4	1.1	.4	1.3	.6
La Palma	575	5.6	15.8	14.9	17.9	36.2	4.9	.2	1.2	.5	1.2	1.6
Hierro	391	5.4	14.8	15.1	13.8	43.5	4.1	—	1.0	.5	.5	1.3

archipelago. They are not unlike those of the Mediterranean countries, with high proportions of annuals. Only the shrub and chamaephyte classes are higher than in most spectra from the region.

The significance of the life form classification is driven home by the surprising conformity of the biological spectra from different islands, even though their floristic make-up and richness of the flora are very different. So close is the resemblance that differences in the percentages of shrubs, chamaephytes and geophytes, and of the minor groups, may well be mere chance deviations. Only the percentages of trees and hemicryptophytes differ significantly ($P < 0.05$), while the differences in distribution of the therophyte class are highly significant ($P < 0.01$). These conclusions are based upon chi square distribution analysis of the actual numbers of species, as outlined by Greig-Smith (1957).

A comparison of the spectra of different islands by statistical means shows that the 5 western islands (Gran Canaria, Tenerife, Gomera, La Palma and Hierro) do not deviate significantly from the spectrum of the Canaries as a whole. But Lanzarote and Fuerteventura both show highly significant differences with the overall spectrum.

Climatic Factors

Raunkiaer has devoted much space to climatic interpretations, particularly of the ratio of hemicryptophytes to therophytes in the Mediterranean. To explain the significant differences between the spectra of the Canary Islands, climatic differences should first be examined. Of key importance is the great climatic diversity on the high central islands. Tenerife (elevation 3,711 m) has at least 4 major climatic zones, including a cloud belt between 300 and 1,500 m on the North coast (Lems 1960a). Lanzarote, one of the eastern islands, is much lower and uniformly dry. Table II shows that it is possible to correlate rather closely the area of the cloud belt on each island, or the entire area above 300 m, with the percentage of tree species, and with the ratio of hemicryptophytes to therophytes. Gomera, the island with the highest percentage of its area in the cloud belt, also has the highest percentage of trees. The two eastern islands, without a true cloud belt and with only 26% of their total area above 300 m, have the lowest percentage of trees and by far the lowest ratio of hemicryptophytes to therophytes. This trend again confirms Raunkiaer's old contention that a shift towards dry climate is correlated with a shift towards annual plants.

Table II. Comparison of climactic areas and certain life form features of the Canary Islands

Island:	Total land area (sq km)	% above 300 m elev.	% in the cloud belt	H/Th quotient of life forms	% trees in the flora
Lanzarote	873	26	0	.23	3.0
Fuerteventura	1725	26	0	.26	3.7
Gran Canaria	1534	70	30	.40	4.2
Tenerife	2060	76	22	.49	5.0
Gomera	378	76	45	.51	6.1
La Palma	728	82	35	.50	5.6
Hierro	277	66	30	.32	5.4

Other Factors

However, no explanation of a life form spectrum can be as simple as that. Even in areas of uniform climate, habitats are occupied by stratified vegetation containing many life forms. The fact is that therophytes, although presumed to be correlated with desert climates, are also typical of open habitats under human influence. And in areas where the human impact goes as far back as it does in the Mediterranean, climatic interpretation of the prevalence of annuals in the flora must be handled with care. Lanzarote, with its therophyte "climate" was also the first to be extensively settled, and has perhaps been grazed and browsed longer than any of the other islands. On the other hand, Gomera has never been an important commerical port. Only recently have its harbor facilities been improved to accommodate ships larger than fishing vessels. Consequently, it lacks some of the annual weeds and waifs that crowd around the busy harbor towns of Tenerife and Gran Canaria. Life form spectra reflect not only the sum of ecological factors, including climate and human influences, but the historical factors of transport and introduction of new species from abroad.

Endemism and Life Form

If such plants as weeds and camp followers affect the biological spectrum of the Canary Islands, what is the life form situation among the endemic species? To answer this question I have calculated the spectra of the endemic, the Macaronesian and the immigrant elements separately. The result of this distinction is very striking (Fig. 1). The spectrum of the endemic element has a totally different aspect from that of the immigrant element, while the Macaronesian group of species, though small, shows again a different spectrum. The great majority of endemic species are shrubs and small bushes (chamaephytes); the immigrant group, although represented in all classes, consists mostly of annual and perennial herbs.

To explain the spectrum of the immigrants in the flora, one need only peruse the available compilations of biological spectra from North Africa and other Mediterranean countries (Raunkiaer 1934, Cain & Castro 1959). They are closely similar, which means that the immigrant element could be a random sampling derived from the flora of the coasts of the southern Mediterranean region.

But the endemic spectrum of the Canaries, with its high values in the shrub and chamaephyte classes, is not paralleled anywhere else. It is reasonable to presume that while the immigrant species are the most recent addition to the flora, the endemic and Macaronesian ones must have been on the scene longer. The great diversification within some of the shrubby groups indicates that they are among the oldest residents of the islands (e.g., *Descurainia,* 6 spp.; *Crambe,* 8 spp.; *Aeonium,* 32 spp.; *Euphorbia,* 10 spp.; *Limonium,* 18 spp.; *Echium,* 20 spp.; *Sideritis,* 16 spp.; *Chrysanthemum,* 14 species; *Centaurea,* 12 species; *Sonchus,* 23 spp.). The explanation of the strange life form spectrum of the endemic element must lie in conditions on the Canary Islands in the far distant past.

The older view, held by European botanists who came to the Canary Islands to marvel at the development of shrubs in "herbaceous" genera such as *Echium, Sonchus, Sideritis, Carlina,* etc., was that the environment of the islands was so favorable that previously herbaceous species became tall and woody (cf. Schenk, 1907; Rikli, 1912; also Johnston, 1953, on *Echium*). Yet it is difficult for an ecologist who has visited the islands to imagine an environment in which shrubby plants are

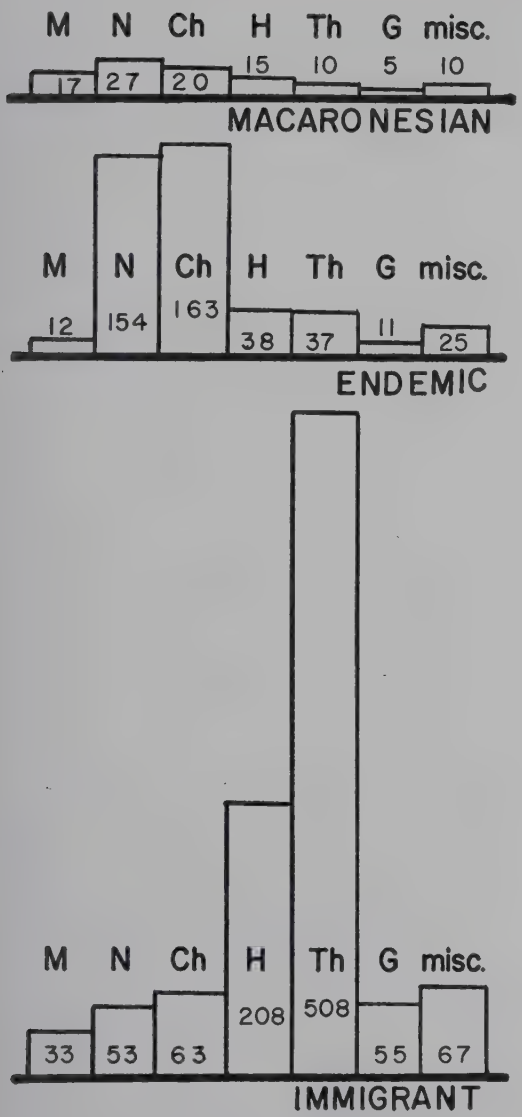
M N Ch H Th G misc.
17 27 20 15 10 5 10
MACARONESIAN
M N Ch H Th G misc.
12 154 163 38 37 11 25
ENDEMIC
M N Ch H Th G misc.
33 53 63 208 508 55 67
IMMIGRANT

FIG. 1. Life form spectra of the Macaronesian element, the endemics and the immigrant species in the Canarian flora. Symbols explained in the text; numbers indicate actual number of species in each category.

favored to the exclusion of herbs; especially since at the present time these life forms live in peaceful coexistence in the same habitats.

The other interpretation is that these endemic plants represent a local development of a primitive Angiosperm flora, in which annuals and other specialized herbs had not yet evolved. According to Hansen (1956) the fossil record of Angiosperm life forms confirms such conditions. The view that these Canarian plants are primitive in form rather than a specially adapted "epharmonic" phenomenon has been promulgated by Meusel (1952). The peculiarities of the biological spectrum of the endemic species are wholly compatible with this view.

CONCLUSION

The presentation of a new set of biological spectra, and its correlation with various environmental forces, is nothing novel, even if it adds to the total knowledge of life forms and statistical plant geography. But I have pointed out some problems and possibilities in the analysis of endemic species and their comparison with the spectrum of immigrants. If the same were done with the floras of other oceanic islands, of continental islands and of mountain ranges with endemic species, we should be in a better position to compare and interpret the effects of endemism on life form spectra.

SUMMARY

1. The life form classification of Raunkiaer has been applied to the flora of the Canary Islands, comprising 1531 species of vascular plants.

2. The calculation of biological spectra for each of the islands shows certain significant differences in the presence of tree species, hemicryptophytes and therophytes on different islands.

3. The presence and extent of a cloud belt on the islands is correlated with life form spectra. The effect of human settlement and the introduction of annual weeds has probably influenced the spectrum.

4. A separate study of the endemic species shows that their life form spectrum differs significantly from the immigrant group. The prevalence of shrubs is discussed in the light of the evolution of woody and herbaceous plants. The spectrum again confirms that the islands harbor ancestral life forms, while the recent immigrants are more highly specialized.

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QUANTITATIVE STUDIES OF THE REMOVAL OF LITTER AND DUFF BY FIRE UNDER CONTROLLED CONDITIONS[1]

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INTRODUCTION

Fire has held a fascination for man ever since he became aware of its usefulness and its danger. His attitude toward fire has often been based on psychological, rather than ecological factors. Various studies and observations have shown that fire, in certain areas and under certain conditions, may be beneficial to the maintenance of certain types of plant communities and the perpetuation of certain plant species (Stone 1951, Stone and Juhren 1951, Mason 1955, Sweeney 1956). Others have shown that fire can be used as an effective tool in forest and range management (Weaver 1957, Uggla 1958, Biswell 1959a, 1959b, Schultz and Biswell 1959). If fire is misused it can be harmful, of course. The literature on fire has been thoroughly reviewed by Shantz (1947), Sweeney (1956) and Ahlgren and Ahlgren (1960).

With the increasing interest in prescribed burning, additional quantitative data may aid those who wish to use fire as a tool to improve game habitats, increase tree reproduction, modify the forest stand, and decrease fuels and the frequency of devastating wildfires.

The forest floor after prescribed burning is generally covered with varying amounts of litter and duff not consumed by the fire (Fig. 1). In an attempt to determine the actual loss of such organic material as a result of fire, quantitative studies were made, using broadcast burning techniques. Broadcast burning is done when the trees are dormant and the soil is wet or moist. This will be soon after rain when the top pine needles are dry enough to carry a surface ground fire. The fire is usually set on ridges and is permitted to burn slowly down hill.

FIG. 1. Remains of litter and duff following prescribed burning in ponderosa pine.

[1] Cooperative project with California Dept. of Fish and Game. Federal Aid in Wildlife Restoration Act Project, California 51-R.

The tests were made in a ponderosa pine forest at Hoberg's in Lake County California, during the spring of 1959. The dominant tree there is ponderosa pine (*Pinus ponderosa*). The most important secondary species are California black oak (*Quercus kelloggii*), Douglas-fir (*Pseudotsuga menziesii*), and sugar pine (*Pinus lambertiana*). The most abundant shrubs are nonsprouting manzanitas (*Arctostaphylos manzanita* and *Arctostaphylos canescens*), Lake County form of deerbrush (*Ceanothus integerrimus* var. *Californicus*), California coffeeberry (*Rhamnus californica*), and poison oak (*Rhus diversiloba*). In some spots the shrubs grow in nearly pure stands intermixed with the pine; in other places they are scattered in the understory of trees. In many places, old shrubs have died beneath dense stands of trees. A large variety of broadleaf herbs, including bracken fern, and many legumes and grasses are found on the forest floor, but are sparse in dense stands of trees and shrubs. From 3 to 8 yrs before the present studies, much of the area had been cleared of heavy debris by prescribed burning, so that the forest was open and park-like. The open nature of the experimental forest was such that when a wildfire burned through this area in 1955 it caused little or no damage to the trees there. However, when it reached the adjacent "natural" forest, the fire crowned and did extensive damage (Biswell 1959).

The soil type at Hoberg's is Salaminas gravelly loam. This soil is formed in place from andesitic and related igneous rocks. It is slightly to moderately acid and has a depth of 3 to 4 ft with very little differentiation in the profile. The soil is moderately permeable and well drained. Within the study area some of the sites were quite rocky, whereas others were relatively free of rocks. The seasonal precipitation is normally about 60 ins. The respective minimum and maximum elevations are 3000 and 3400 ft (915 and 1036 m).

METHODS

Four experimental plots were established at different locations so that measurement of litter and duff would show some of the variability likely to occur within any given fire area. The areas were: (1) level (elev. 3100

ft) under a moderately dense stand of trees; (II) level open (elev. 3400 ft) at the edge of the forest; (III) and (IV) adjacent and on a west-facing slope (about 10°; elev. 3000 ft) under a moderately dense stand of trees. At each experimental plot, 5 series of six 2×2 ft squares were established. After all organic material was removed down to the mineral soil for each square, series 1 through 4 were reconstituted with definite amounts of organic litter and duff as shown in Table I. Series 2 had 100% more litter and duff than series 1, and series 3 and 4, 200 and 300% more, respectively.

TABLE I. Reconstituted amounts of litter and duff for each of 6 squares in each series

Series	Litter (grams)	Ave. depth (cm.)	Duff (grams)	Ave. depth (cm.)
1	454	4.5	908	1.0
2	908	6.4	1816	1.9
3	1362	9.6	2724	3.5
4	1816	12.7	3632	5.7
5	Control	8.9	Control	4.5

Burning of the experimental plots followed established procedures for broadcast burning. Fire was always set along the entire width of the plots and allowed to burn within previously established fire lanes (Fig. 2). When the entire area of each plot had burned it was allowed to cool for 2 hrs.

After each series was reconsituted, squares 2 and 5 were used for sampling to determine moisture percentages of litter, duff, and surface soil prior to and immediately following the fire. Environmental conditions that might have the most influence on each experimental burn were recorded immediately before and during each fire (Table II). After each burn, the remaining litter and duff were carefully collected from each square on the plots and weighed. This made it possible to determine the actual loss of organic material for each experimental plot. The small amounts of ash mixed between the litter and duff layers when the remaining organic material was recovered for weighing constituted such a small percentage of the total weight that it was considered insignificant.

FIG. 2. Prescribed burning of Plot IV in an open park-like ponderosa pine forest at Hoberg's.

TABLE II. Summary of environmental data for plots during experiment

Plot No.	I	II	III	IV
Set	2/23/59	2/28/59	3/ 7/59	3/ 7/59
Samples	2/28/59	3/7/59	3/14/59	3/14/59
Fuel moisture:				
Litter	24.1%	14.0%	9.7%	10.3%
Duff	44.3%	18.2%	25.7%	22.0%
Burned	2/28/59 11:40 A.M.	3/ 7/59 10.35 A.M.	3/14/59 10:35 A.M.	3/14/59 12:02 P.M.
Burning time*	14 min.	12 min.	20 min.	8 min.
Air temp.	64° F. (18° C.)	62° F. (17° C.)	50° F. (10° C.)	56° F. (13° C.)
Rel. hum.	40%	38%	30%	24%
Wind	slight & var.	gusty to 10 mph	none	slight & var.
Site	level-protected	level-open	10° slope burn downhill	10° slope burn uphill
Elevation	3100 ft. (945 m.)	3400 ft. (1036 m.)	3000 ft. (915 m.)	3000 ft. (915 m.)

* 2 hours allowed for cooling before weighing remaining litter and duff.

RESULTS AND CONCLUSIONS

Quantitative measurements of loss of organic material following prescribed burning of the 4 experimental plots revealed several interesting facts. In no instance did the fire destroy all of the litter or duff. The average loss of litter was 75.87% and of duff, 22.94%. The greater loss from the litter layer was to be expected because (1) the litter was relatively loose, whereas the duff was finer and more compacted, (2) the moisture content of the litter was lower than that of the duff, and (3) position of the 2 layers resulted in a difference in oxygen available to the surface and subsurface material.

The litter layers on plots I and II showed a difference in loss of 8.8% (Table III). The plots were both level, and the elapsed time for burning was approximately the same. The variables between the 2 plots were fuel moisture and wind (Table II). The lower fuel moisture and higher wind velocities could account for the increased litter loss on plot II. The differences in oxidation of litter on plots III and IV (24.1%) can be attributed to the slope and to difference in elapsed time for burning. Fire burning down-slope took 20 min to cover plot III, whereas fire burning up-slope

TABLE III. Average loss of organic material from each plot by prescribed burning

Plot	Angle of slope (percent)	Loss of litter (percent)	Loss of duff (percent)
I.....	0	74.5	27.7
II.....	0	83.3	31.5
III downhill burn	10	85.1	15.4
IV uphill burn...	10	61.0	17.1

covered plot IV in 8 mins. The rapidity of the fire on plot IV did not allow the same amount of litter oxidation as on plots I, II, and III. The factors of fuel moisture and wind showed only slight differences between plots III and IV, and are considered insignificant.

The data from plot II, as compared with those for plot III show that loss of litter was not greatly different between a burn on level ground or a fire running downhill (1.8%). This similarity of fuel consumption was considered to be coincidental and the result of some compensating factor, probably wind. The greater difference between plots I and III (10.7%) was interpreted as resulting from the greater difference in fuel moisture and time with no compensating factor such as wind (Tables II and III).

When the data on oxidation of the duff layers were compared for the 4 plots (Table II) plots I and II showed little difference (4.8%), as did plots III and IV (1.7%). However, the much greater loss from the duff layers on the level plots (I and II) compared with that lost from the plots on the slope (III and IV) cannot be readily explained from these experiments. Fuel moisture differences between the litter and duff layers for each plot might have been significant, but this is not clearly indicated by the experiments even though it is suggested by the case of plots II, III and IV (Fig. 3). The fuel moisture difference between litter and duff layers was lowest for plot II, which also showed the highest loss from the duff layer. The lowest loss occurred on plot III, which had the greatest difference in fuel moisture between the 2 layers.

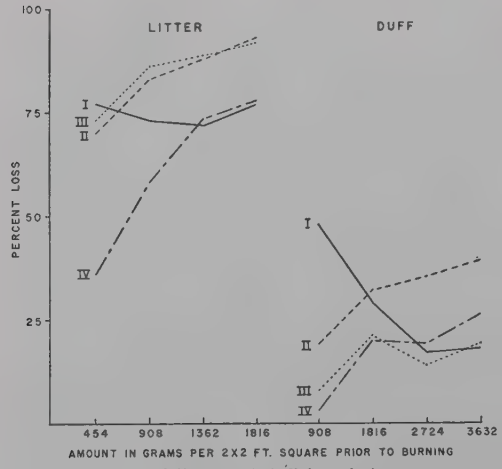

FIG. 3. Loss of litter and duff in relation to amounts present prior to prescribed burning for each of the four plots.

The variation in loss of organic material in relation to the amounts present prior to burning is shown in Figure 3 for each of the 4 plots. Again, variations of the curves for the various plots might have resulted from fuel moisture differences.

One of the most striking aspects of this study was the great variability in organic material burned from the different squares within the same series on each of the 4 plots. For example, on plot I, where 454 g of litter covered each square in series 1, the amount of loss ranged from 287.5 to 375.4 g. This variability occurred even though the squares for each series were adjacent to one another, contained the same amounts of organic materials, and were covered by the same fire. Similar variations were recorded for all of the plots. Such variability is probably due to the fact that, as it burns, fire induces conditions in addition to those already present within a given area.

The control series (Table I) on each of the plots showed differences in amounts of organic material present on the forest floor. The range of variability on plot I was 430.5 — 1589.0 g. The range of variability for all plots was 198.8 to 1589 g. The range in loss due to oxidation was 39.7% to 60.5% for litter and 4.3% to 28.5% for duff on the control series on all plots. The variability in amounts of organic materials throughout the forest floor would, in itself, result in greater irregularities in the oxidation of organic materials present in any given location. This insures the presence of areas, however small, where species can survive and maintain themselves where fire is a common factor of the environment.

SUMMARY

Quantitative studies of the removal of organic materials by prescribed burning techniques were made in a ponderosa pine forest at Hoberg's in Lake County, California. These studies showed that:

1. In no instance was all of the organic litter and duff destroyed by controlled fire on 2×2 ft squares.

2. The average loss of litter was 75.87% and of duff, 22.94%. In all cases sufficient litter and duff remained after prescribed burning to cover the soil.

3. There was great variation in the oxidation of organic materials by fire among the different experimental plots and within individual plots.

4. In the control series there was no uniformity in amounts of organic materials covering the forest floor, nor in the amounts consumed by the fire under relatively uniform conditions.

5. There was evidence that the percentage loss of litter and duff increases as the amount available increases. However, the actual amount of litter and duff remaining after prescribed burning was greatest where the litter and duff were deepest and were wet in the lower portions.

6. The results indicate that fire can be used under controlled conditions in forest management to reduce wildfire hazards, and for other reasons, without destroying all the litter and duff and exposing the soil.

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While early vegetation studies in Russia were influenced by the ideas developed in western Europe, the influence of a few dominant figures in Russian botany and forestry resulted in the establishment of a Russian school of phytocenology which differs in several respects from the European schools of phytosociology.

Some of the first phytosociological studies of the vegetation of Russia were made towards the end of the last century, when Korzhinskii (1888-1891) studied plant succession in relation to the replacement of grassland by forest. With the development of plant sociology in Europe the terms "phytosociology" and "association" were introduced in studies of Russian vegetation by the Polish botanist Paczoski (1896) and the Russian Krylov (1898). Studies of natural vegetation were largely centered around the vast forest resources of northern Russia and much influence was carried by the forester Morozov, one of the great pioneers in Russian vegetation studies. Morozov (1913) viewed forest associations as social and geographical phenomena, the social part covering the interactions between plants making up the association, and the geographical part considering the relations between vegetation and the physical environment. Among the factors of the physical environment the soil has traditionally received a large share of attention in Russia.

By 1930 the study of vegetation in Russia had developed sufficiently to become differentiated from the western European schools of phytosociology and the newer terms "phytocenology," proposed by Gams (1918), and its synonym "geobotany" were adopted to describe the science of the study of vegetation and its relation with environment. Thus phytocenology becomes equivalent to what is known in the United States as synecology; the Russian use of the term ecology is almost exclusively reserved for autecology.

Sukachev (1954) defines the place of phytocenology within the larger sphere of the total environment. Besides phytocenology, the study of plant communities, there is zoocenology, the study of animal communities. These communities are combined into a biocenose, or the community of living organisms. The external, physical environment forms the geocenose, which is divided into the edaphotope, covering the influences pertaining to soils and parent materials, and the climatope, considering climatic influences. The biocenose and geocenose are combined into the biogeocenose, covering the whole environment of an area determined by a uniform phytocenose.

Sukachev (1935) considers the phytocenose a stand of actual vegetation, a grouping of plants with reciprocal dependence, characterized by definite relations with the environment and a definite composition and structure. The phytocenose has its own internal environment, dependent on and related to the vegetation, the result of the cumulative effect of the interactions between the individual species. The subdivisions of a phytocenose are synusiae, separated on the basis of spatial or temporal features of the plants in each synusium. The association, according to Sukachev, is the type-phytocenose, a grouping of similar phytocenoses united by the similarity of reciprocal relations among species in each phytocenose as well as between species and their physical environment. Thus Sukachev places primary importance on the interactions between the individuals which make up the plant community; all other influences on the plant community are considered external and indirect.

Alekhin (1935) has a different viewpoint which adheres more closely to the Scandinavian school of phytosociology as defined by du Rietz (1930). Alekhin allots most importance to analytical methods of measuring vegetation by floristic composition, and gives little consideration to relations between vegetation and environment. Alekhin's association is the actual plant community, equivalent to Sukachev's phytocenose, and an association is divided into sociations characterized by a definite floristic composition and representing layers of vegetation.

Several other viewpoints with only minor variations

in emphasis from Sukachev's theories include those of Ramenskii (1935) of the Institute of Economic Plants in Moscow, of Reverdatto (1935) based on the works of Krylov in Siberia, of Grossgeim in Caucasia and of several others centered around the Universities in Alma-Ata, Kazan, Kiev and Minsk.

With the emphasis on the internal environment of the phytocenose, many interrelations between plants have been studied. The studies in plant competition of Clements, Weaver and Hanson (1929) are widely quoted. Sukachev (1953) has summarized the accumulated knowledge on intraspecific and interspecific relations. Intraspecific competition is mainly within biotypes, groups of individuals which are genetically similar. In widely-spaced vegetation the variation between biotypes is greater than in dense vegetation, but even with greater variation the differences in ecological and physiological reactions are always elusive and the exact causes of the survival of one biotype and the failure of another are difficult to determine.

Sukachev considers interspecific relations most important in determining the structure and equilibrium within a phytocenose. They are created by the overpopulation of an area by plants and the relations can be either competitive or beneficial depending on the various species involved. Interspecific competition produces plant succession by causing the death or failure of reproduction or establishment of some species. While interspecific relations are most important within the phytocenose as a whole, intraspecific relations play a major role within each, sometimes largely monospecific, layer of the phytocenose.

Finally Sukachev states that although plant interrelations vary with the ecological and biological characteristics of the plants themselves, they are also strongly influenced by the conditions of the physical environment and the variations in vegetation density.

Succession is interpreted as a change in the dynamic phytocenose as internal and external environments change. Although Clements (1938) is widely quoted as the source of the succession concept, few of his views on the subject are accepted by the Russians and they deplore his weakening of the term climax by modifying it with so many prefixes denoting non-final stages. The Russians have coined the term "conclusive stage" to indicate the final stage of successional development. In their view, as explained by Bykov (1957), succession is mainly the result of internal influences or "endodynamic" causes. Thus the invasion of an area by a new species changes the internal environment through modification of plant interrelations, and the phytocenose adjusts itself to a new equilibrium through succession. But even as a given succession presents an example of endodynamic changes, a large role is also played by the modification of the physical structure of the developing soil and such influences of "exodynamic" character are always present. The plant community continues its development until internal equilibrium is reached, this equilibrium is influenced by the external environment but never dominated by it.

The most widely used system of vegetation classification is the one adapted by Alekhin (1944) from the physiognomic-ecological classification system of Brockman-Jerosch and Ruebel (1912). In Table I an example of the Russian system is given showing the classification of a pine forest. Other classification systems have been set up on a genetical basis related to the origin and development of the vegetation type. Leskov

TABLE I. An example of the Russian system of vegetation classification proposed by Alekhin

Vegetation type—Lignosa (forest)
Formation class—Aciculisilva (needle-leaved tree forest)
Formation—Pineta silvestris (all forests with *Pinus silvestris* as dominant)
Association group—Pineta-Hylocomiosa (pine forests associated with *Hylocomium* mosses)
Associations—Pinetum myrtillosum (*P. silvestris, Hylocomium schreberi, Vaccinium myrtillus*)
Pinetum Vitis-idaeosum (*P. silvestris, H. schreberi, Vaccinium vitis-idaeus*)
and others
Sociations—Pinus silvestris
Hylocomium schreberi
and others

(1943) classified the *Abies* forests of Russia on such a genetical basis. He considered that the evolution of the communities ran parallel to the evolution of their influent species and consequently he based his classification on the latter.

Sukachev (1944), in a paper translated and edited by Raney and Daubenmire (1958), points out that although Leskov's classification is valid for *Abies* forests, his basic assumption does not hold true in many other vegetation communities where the evolution of the dominant species is not related to the development of the community. Sukachev recognizes two main types of community development: cenogenesis and syngenesis. Cenogenesis refers to the slow evolution of the community in close relation to the evolution of the majority of the species present in that community. Syngenesis refers to the successional derivation of a community composed of species of varying origin.

The classification system proposed by Sukachev recognizes the various successional stages in vegetation development and is based on features appearing in the course of the joint existence of the species making up vegetation units and not on the ecological and biological features peculiar to the species themselves. The properties of the synusiae differing from each other in relation to rooting depth, seasonal aspect, denseness, etc. become important.

Thus Sukachev (1928) divides the spruce forests of European Russia into the following community groups, or associations: Piceeta hylocomiosa
Piceeta polytrichosa
Piceeta sphagnosa
Piceeta herbosa
Piceeta fruticosa

Of these different spruce communities Sukachev considers the Piceeta hylocomiosa the fundamental association. It is most persistent and the interrelations between the elements of the community are most perfect. The dominant tree is truly dominant in its influence and the undercover of mosses is especially suited for its regeneration. With environmental changes towards increasing bogginess a succession of less well-integrated communities takes over leading to Piceeta sphagnosa and then to communities of the Pinetum group. Sukachev links the various associations into a successional series based on the development of new plant interrelations as environmental changes cause the development of certain strata with their consequent influence on the internal environment of the community.

SUMMARY

The study of plant communities, or synecology, is called phytocenology in Russia; the term ecology is reserved for autecology. The phytocenose is a grouping of plants with reciprocal dependence; it possesses its own internal environment dependent on the species of which it is composed. A phytocenose is divided into synusiae distinguished on the basis of spatial or temporal features. The association is the type-phytocenose, a grouping of phytocenoses united by a similarity in the reciprocal relations among the species of each phytocenose. Primary emphasis is placed on the interrelations between the individuals of the plant community and succession is interpreted on the basis of changes in the internal equilibrium of the phytocenose. In the classification of vegetation the original Russian system proposed by Alekhin is based on floristic composition of actual stands, but a classification system proposed by Sukachev is based on the recognition of successional stages and the development of related associations.

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A SIMPLE METHOD OF MEASURING INTEGRATED LIGHT VALUES IN THE FIELD[1]

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Light sensitive diazo compounds form deeply colored addition compounds on short exposure to ammonia vapor. This principle has been used to manufacture the range of 'photographic' copying materials brought out by the Ozalid Company and other firms. Paper coated with a diazo compound together with a suitable coupler, is used to make direct positive 'blue prints'; upon exposure to light the unmasked area of paper is bleached. After a dry development in ammonia vapor, the unbleached area becomes brightly coloured. This process can be used as a simple and inexpensive integrating light meter. A stack of 15 sheets of Ozalid paper is stapled into small booklets, which are placed in transparent plastic dishes to protect them from rain, and positioned in the field. After a given exposure time, usually one day, the booklet is developed in ammonia vapor and the penetration of light through the stack of papers is measured by the number of layers bleached. Calibration against a standard light measuring device allows the conversion of this number into a measure of light energy received.

While photo-electric integrating light meters (e.g., Blackman *et al.* 1953) are capable of providing highly accurate measurements, the expense of having a number sufficient for adequate simultaneous sampling of various habitats is prohibitive. Chemical light meters, using anthracene (Dore 1958), potassium iodide (Pearsall

[1] Contribution No. 110 from the Plant Research Institute, Research Branch, Canada Department of Agriculture, Ottawa, Ontario.

1933), or uranyl oxalate (Atkins and Poole 1930), can be of great value in the field, and they have sufficient accuracy when the variation of the habitat is considered.

Photographic methods have been used for a long time and are easier to read than chemical light meters, which usually require titrations or spectrophotometer estimations. With normal silver halide papers the range of densities obtainable is not very great, and various difficulties have been encountered in calibrations (Matheson 1938). Ozalid paper has the advantage of slow speed and a dry development process. As the action of light is to bleach the paper, rather than darken it, a series of density filters is provided by the stack of paper itself. Large numbers of booklets can be rapidly prepared, the paper is inexpensive and does not require the use of a dark room.

Materials and Methods

Preparation

The type of paper used was Sepia Ozalid paper, No. 33 NT, 8½ × 14 in. A stack of 15 sheets, all placed with the pale yellow coated side uppermost, was stapled down one side and cut into strips. Further stapling and cutting (Fig. 1) resulted in 144 booklets, each about

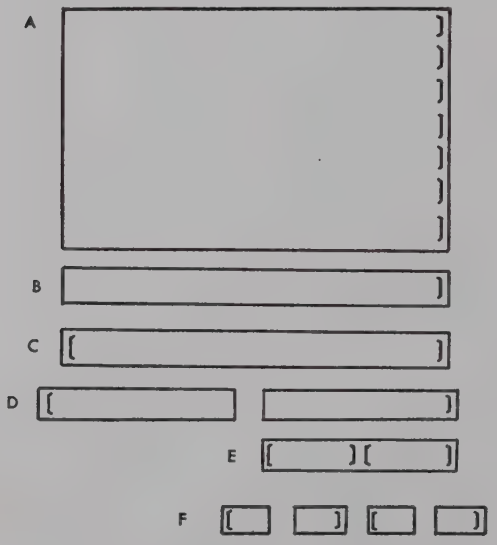

Fig. 1. Diagram of cutting and stapling of Ozalid paper for rapid assembly of booklets.

1 × ¾ in. These operations should be carried out in dim light and the booklets stored until needed in a darkened container away from heat and damp. Plastic culture dishes, 50 × 12 mm, (#PD 5012, obtainable from Falcon Plastic Products, Culver City, Cal. U.S.A.) were used to protect the booklets from rain. A piece of sponge rubber covered with black paper was placed in each dish so that when a booklet was placed on top and the lid replaced, the sensitive surface was held flat against the inner surface of the lid. A piece of black paper with a central hole about ⅜ in. in diameter, allowing light to reach the sensitive surface of the booklet, was fitted inside the lid (Fig. 2). Under these conditions there was no fogging at the edges of the booklet.

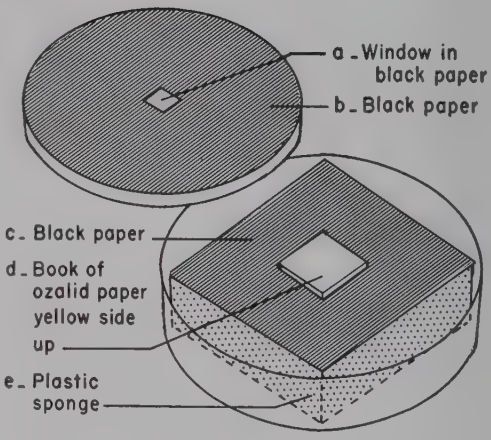

Fig. 2. Plastic dish for exposing Ozalid paper.

Under heavy rainfall the dishes leaked somewhat; this could be prevented by binding the edges of the dishes with waterproof tape. These operations should be carried out in dim light, and the loaded dishes may be prepared in advance and stored in dark containers for use in the field. Loading may also be carried out in the field, even in direct sunlight, by inverting the lid of the plastic dish on the ground, tearing off the top sheet of a booklet (as it will be slightly fogged after removal from the dark container) and rapidly placing the booklet sensitive side downward over the window in the lid. The base of the dish is then rapidly placed on top of the lid, and the dish turned right-side-up and placed in position.

Exposure

The dishes are placed in position either directly on the ground or supported at the desired level, and left for 24 hrs. The dishes should be level, but in practice, provided there is no directional bias, small variations from the horizontal are not important. For periods of exposure longer than 24 hrs., a piece of neutral grey filter of the required density may be placed above the paper. Using different densities of filter will give the required sensitivity. A suitable material for the filter is Cinemoid plastic, made in a range of densities, which has the advantage of being cheap and fade resistant. This is obtainable from Strand Electric and Eng. Co., 755 Yonge Street, Toronto 5, Ontario. To measure the light falling on a spherical, rather than a flat surface, which is often preferred in ecological work (Middleton 1953), half a celluloid table tennis ball can be cemented on top of the lid.

After exposure, the dishes are taken to a dimly-lit place, and the booklet removed and labelled. These may be stored in the dark or developed at once in ammonia vapor. A useful developing jar can be made by boring two small holes in the plastic lid of a wide-mouthed 5 lb glass chemical jar. A piece of wire is then pulled through the holes, and a wire basket suspended from the underside of the lid. Sufficient room should be left for easy insertion of the booklets into the basket. About 25 ml of concentrated ammonium hydroxide are then poured into the jar, and the screw cap replaced. The length of the wire should be adjusted so that the book-

lets are suspended about one inch above the surface of the ammonia. Development time should be about 10–20 minutes, to give time for the ammonia vapor to penetrate the booklets but there is no danger of overdevelopment. The number of paper layers affected by light can then be counted. The penetration of light closely follows Lambert's law of absorption; the number of layers bleached is proportional to the logarithm of the light energy received. Under a full day's summer sunlight the 11th or 12th page shows a faint bleaching.

Calibration

A calibration curve for the Ozalid meter is obtained by making a series of exposures to a given light source and equating these readings with measurements made by a standard light measuring instrument. If an illumination meter is used, an absolute energy value can only be obtained if both the response curve of the photocell and the spectral distribution of the light source are both known. The calibration methods described here made use of a Weston Sunlight Illumination meter, model 756, with a flat light target and quartz filter. The response curve of this instrument is given by the Weston Co., 1952, and the spectral distribution of light from various artificial sources by Weitz 1950. A more precise alternative is to measure the light energy directly in absolute units, using a combination of thermopile and filters such as those described by Friend (1960); calibration by both methods was used in Figure 3. Because of the general availability of the Weston instrument, further descriptions of calibration are in terms of illumination units. For calibration in absolute energy units the procedure would be similar.

The precision of the meter can be greatly increased by estimating 'between paper' readings. The time is determined at which exposure to a constant light source just visibly bleaches the third layer in the booklet, as shown after development by viewing the paper by back illumination. This exposure time is about 6 minutes for white fluorescent light of 1,500 ft-c intensity. These second and third layers in the booklet give the 0 and 10 range of ten 'between paper' divisions. Intergrades are obtained by exposing another booklet so that the bleaching effect of light is just visible in the second layer. The time interval between this bleaching of the third and second layers is then divided logarithmically into 5 intervals. Exposure of further booklets for these duration provides 4 integrades. The series of 6 papers is then mounted on cardboard, so that they can be viewed by back lighting for easy comparison with test papers. This scale should be kept in an envelope to prevent fading. The calibration curve in Figure 3 was prepared by matching against such a standard series.

Calibration of the dishes should be carried out using a light meter with a target similar to that used on the Ozalid paper meter, ie., with or without neutral filters or a hemispherical collecting surface. The light meter used in the calibration should not be cosine corrected, unless such a correcting filter has also been built into the Ozalid meter. Natural daylight may be used as a light source for calibration; the amount of light energy received by a series of exposures of paper can be determined by an integrating light meter. Alternatively, light readings can be taken with a Weston type foot candle meter at 15 minute intervals (during a cloudless day preferably) and the amount of light energy received by any one exposure series obtained by integration of the appropriate readings. A calibration curve was fitted

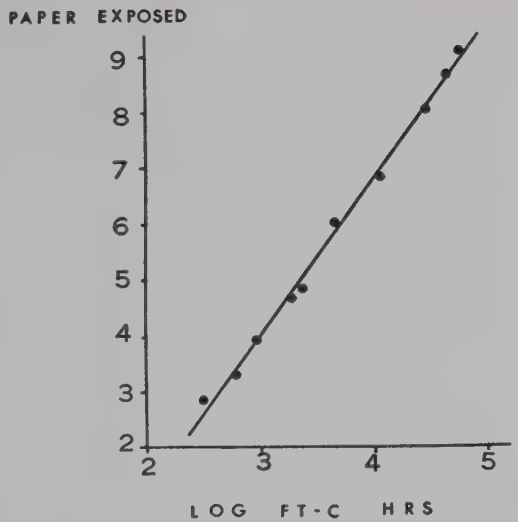

Fig. 3. Calibration of Ozalid paper meter in terms of ft-c hours. Standard cool white fluorescent light (General Electric Co.) was used at an intensity of 622.2 ft-c, as measured by a Weston Illumination meter, model 756, with a flat light target with quartz filter. With the same light source one ft-c is equivalent to 6.72 microwatts in the visible spectrum from 400 to 720 mμ, as measured by a G2 Kipp Solarimetric thermopile with suitable filters. From the regression, $\log_{10}$ ft-c hours $= \frac{\text{paper reading} + 4.47}{2.83}$. Each point is a mean of five values, and the coefficient of correlation was .993, significant at the .1% level.

to such data, for paper exposed for 1, 2, 4, 8, 16, 30 mins. and 1, 2, 4 hrs. A straight line regression was fitted, of the formula $\log_{10}\ x = ay + b$, where $x =$ light energy in foot candle-hours as determined by a Weston meter, $y =$ number of layers of paper bleached. Each point on this graph was derived from the mean of 5 replicate Ozalid meters. From this regression, ft-c hours $=$ antilog $_{10}$ (paper reading $+ 3.41$) $- 2.414$. The correlation coefficient was .998.

If it is desired to measure light of spectral quality different from that of sunlight a separate calibration should be carried out. An example of such a calibration obtained by exposing paper for different times to a given intensity of white fluorescent light is given in Figure 3.

Spectral Sensitivity and Accuracy

Wavelengths around 410 mμ are strongly absorbed by the sensitive layer on the Ozalid paper (Table I). Shorter wavelengths are active in bleaching the Ozalid compound, but are filtered out by the paper. This absorption peak is close to the region of absorption in the blue by the living leaf (Moss and Loomis 1952).

Changes in the spectral emission of the sun during the day are not sufficient to affect accuracy. A series of 5 consecutive exposures for one hour periods, starting at noon, showed no significant departure from the calibration curve. Any possible errors caused by the much altered spectrum of the sun at sunset or sunrise can

TABLE I. The light absorbed by the sensitive surface of Ozalid paper when sunlight is passed through layers of bleached paper

Wavelength mμ	Absorption as % of peak at 410 mμ
440	12.4
430	56.0
420	94.8
410	100.0
400	97.4
390	83.1
380	66.1
370	25.1
360	34.9
350	12.7

be avoided by placing the Ozalid meters in the field between mid-morning and mid-afternoon. As the bleaching of the paper is related to the logarithm of the light energy, the greatest number of layers will then be bleached when the sun's spectrum is reasonably constant.

The sensitivity of the method is not very great. Using the 'between paper' readings, the light received during the course of a sunny summer day provides a reading of 11 papers, equal to 55 'between paper' readings. Because of the great variability of light conditions in the field, this sensitivity is probably more than adequate. The accuracy of the method is also sufficient for field use; the mean of 10 readings obtained by exposing booklets to the same light intensity (1½ hours sunlight) was 7.1 with a sample standard deviation of ± .021, and a coefficient of variation of 3%.

It is often convenient to record the degree of shading within a given habitat as compared with open sky, and for this purpose calibration in either relative or absolute units will be equally effective. Absolute values for the total daily radiation in the region of the spectrum active in photosynthesis may sometimes be obtained from nearby meteorological stations. Examples of this use of Ozalid meters for measuring the degree of shading within a series of oat crops and in a dense stand of red clover are given below.

Oat plants (at the stage of heading), on July 19-20, 1960, at Ottawa, gave 54% shade at ground level when the density per sq ft was 1 plant, 67% when 2 plants, 71% when 4, and 75% when 8 plants. Per cent shade is 100 (u-s)/u, where u represents integrated light values from an unshaded area, and s denotes values from a shaded area. Each figure given is a mean of 5 replicate light determinations. The first two percentages are significantly different at the 5% level, using Duncan's (1955) test.

Red clover in full flower gave 99.7% shade as shown by the Ozalid meter. The mean of 10 readings taken at noon by Weston Sunlight Illumination meter, model 756, quartz filter, was 15.4 ft-c under the plants. The intensity under the open sky was 9,200 ft-c and the per cent shade 99.8.

Changes in the sensitivity of the paper may occur with age, and a check on calibration should be made at about 2 wk intervals. A convenient way of continuously checking the constancy of paper sensitivity is to expose several meters fitted with neutral filters alongside those exposed to full daylight. The filters should be fade-resistant, and have about 10% transmission. Changes in the calibration curve affecting light values expressed as a percentage of full daylight will then be revealed.

SUMMARY

A simple light meter is described that is suitable for measuring integrated values of light energy under field conditions. A stack of photosensitive Ozalid paper is exposed for daily periods; the amount of light energy received is estimated from the number of layers of paper penetrated by light, revealed after a dry development with ammonia vapor. The simplicity and cheapness of the method allows the use of the large number of replicates needed for adequate sampling of the habitat, and the sensitivity and accuracy are sufficiently high for field use.

ACKNOWLEDGMENTS

Acknowledgments are made to the following associates in the Plant Research Institute: to the former Director, H. A. Senn, and to W. G. Dore, for suggesting the need of a simple light integrating device for field use and for helpful discussions. Thanks are also expressed to W. E. Cordukes for use of the data on shading in oats, and to G. W. Robertson.

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ENERGY VALUES OF ECOLOGICAL MATERIALS

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Since Lindeman (1942) formulated his concept of trophic dynamics, American ecologists have become increasingly interested in the energy relationships of ecosystems. Even though the application of thermodynamic theory to ecology has progressed rapidly (see Odum 1956, Odum and Pinkerton 1955, Patten 1959, Sobodkin 1960), understanding of the energy dynamics of individual populations has been hampered by incomplete knowledge of the energy content of many plants and animals. In energy flow studies it is often necessary to convert biomass to energy by using caloric equivalents obtained from the literature. However, many workers, reluctant to depend upon equivalents, have made their own energy determinations in the oxygen bomb calorimeter. This paper summarizes my analyses of over 400 wild plants and animals collected from the field and over 200 analyses of other workers. These values were previously listed in a mimeographed publication (Golley 1959).

I am indebted to a number of persons who have aided these studies. In 1956-57 equipment for caloric analyses in the laboratories of the Department of Foods and Nutrition, Michigan State University, was used through the courtesy of Dr. Evelyn Jones. Later studies were made in the ecological laboratory of Dr. E. P. Odum, Univ. of Ga. and the work was supported by the U. S. Atomic Energy Commission, contract At(07-2)-10. I am grateful to Dr. Odum for his critical comments during these investigations. I am also grateful to Drs. Lawrence Bliss, Univ. of Illinois; Francesco Trama, Rutgers Univ.; Edward Kuenzler, Woods Hole Oceanographic Institute; Clyde Connell, Valdosta State College, Ga.; and J. D. Ovington, The Nature Conservancy, London for providing unpublished data from their studies.

Methods

The caloric value of ecological materials was determined by burning samples in a Parr oxygen bomb calorimeter. The standard procedure for determining energy values is fully discussed in the Parr Manual (1948).

Since the purpose of the measurements is to provide estimates of energy content of biomass that can be applied to populations of plants and animals in the field, the samples must reflect the variations inherent in field populations. Therefore, vegetation samples are collected from random plots on study areas, dried at 100°C for 24 hours and ground in a Wiley Mill fitted with a 40 mesh-to-the-inch screen. When only the small mill is available, portions from pooled samples from all plots are selected for grinding. The ground tissue is then thoroughly mixed in jars before samples are removed for calorimetry.

Since the amount of body fat (which has a high energy value) varies with age and season in many animals, each age group must be sampled at each season to obtain a caloric estimate that can be applied to the populations at specific seasons. For many groups of animals, e.g., insects collected by sweep-netting, the entire dried sample can be run through the mill. For fleshy animals, such as birds or mammals, specimens are minced in a Waring Blender, the slurry of water and tissue dried in a vacuum oven, and the dried material ground in the Wiley Mill. Extremely fat animals are difficult to handle even with this procedure. With these it is best to extract the fat after vacuum drying then redry and combust the nonfat residue.

The calorimeter is restandardized (the water equivalent determined) every third month, especially when the laboratory temperatures fluctuate widely. The magnesium fuse wire and the total acid corrections are determined for each individual analysis, rather than assumed to be constant, since the amounts of fuse wire used and the acid produced vary widely. For instance, insect samples may require more than 9.0 ml of base to neutralize the acid formed during combustion, while plant material usually requires only 5.0 ml or less. The difference of 4 ml is equivalent to 4 g cal. The amount of fuse wire burned has varied from 9.3-3.6 cm in these studies. Corrections are made by measuring the unburned wire with a ruler (1 cm of burned wire = 2.8 g cal) and by titrating the bomb washings with a sodium carbonate solution (3.658 g $Na_2CO_3/1H_2O$, 1 ml solution = 1 g cal).

The per cent ash in each sample has been determined since 1958. This merely requires drying and weighing the tarred calorimeter cup containing the ash after the tests are completed. The caloric value per gram ash-free weight more accurately reflects differences between materials than the value per gram dry weight because of contamination. Samples of roots and ground litter, in particular, often contain soil which cannot be dislodged by routine washing and if it is included the caloric value will be lowered.

The Parr Manual (1948) states that the American Society for Testing Materials requires 0.3% accuracy for tests of the same material made in the same laboratory and 0.5% for tests made in different laboratories. I have not achieved this degree of accuracy with all types of ecological materials and have accepted as satisfactory a variation of not more than 3.0% between 3 tests on a given sample. All of my analyses have been run in triplicate.

The caloric value of plant materials was tabulated under 3 categories: plant parts, month collected, and ecological community. Comparisons between members of a category were tested by an analysis of variance procedure. Mr. James Fortson, Institute of Experimental Statistics, Univ. of Ga., transformed the data using matrices and the statistics were calculated on an IBM 650 computer. Significance of the difference between values in each separate category was determined with the F-test. Animal caloric values were subjected to an analysis of variance using a desk calculator. Since many values were obtained from the literature or were made before the ash-correction became routine, all are reported as gram calories per gram dry weight.

Results

Table I presents the mean energy values for parts of plants. The differences are significant at the 99% level ($F = 27.72$, d.f. = 4 and 462). Seeds, which often contain high proportions of fat, have the highest values. Long (1934), one of the first to apply calorimetric methods in ecological research, also found that energy values varied for parts of the plant. In the sunflower he found

TABLE I. Average energy values for parts of plants, based on determinations from 57 species (Value g cal/g dry wt)

Part	Number Samples	Average Value	Coefficient Variation
Leaves	260	4229	.116
Stems and Branches	51	4267	.081
Roots	52	4720	.092
Litter	82	4298	.104
Seeds	22	5065	.219

that the values ranged from 4308 g cal/g dry wt for the seed head to 3435 g cal/g dry wt for one of the oldest leaves. The highest values he obtained were for seeds of conifers, which ranged from 5625-7117 g cal/g dry wt.

The seasonal analysis includes vegetative samples from 3 old-field communities: a blue-grass field in Mich., a broomsedge field and young pine stand in Ga. (Table II). Values for the dominant plants in these 3 communities were grouped so that the comparison is between months, irrespective of the species of plants. The analysis of variance showed that significant differences at the 99% level ($F = 2.36$, d.f. $= 11$ and 272) existed between months. The highest caloric values occurred in the fall and winter, presumably from storage of energy in the roots, culms, and seeds. Morrison (1949) reports that in many plants the per cent of crude protein in the green foliage decreases, that of crude fiber and nitrogen-free extract (mostly carbohydrate) increases, while that of ether extract (partly fat) remains constant through the growing season. Accordingly, the caloric value of the foliage should be higher in the spring than in the fall. However, when considering all parts of the vegetation growing in the community the caloric value per gram total vegetation (including roots and seeds) appears to be greater in the fall and winter.

Caloric data are available for the dominant plants in 9 ecological communities, ranging from tropical rain-forest to alpine tundra. The pine community data furnished by J. D. Ovington are from England. The alpine tundra data obtained by L. Bliss are from New Hampshire. The *Spartina* (analysed by C. Connell), the *Andropogon*, and the old-field herb communities were studied in Ga., the *Poa* community in Mich., and the rain-forest and mangrove forest in Puerto Rico. The values in Table III are mixed-species averages of all the data available for the dominant species; they are not average weighted by the importance of individual species in the phytosociology or biomass composition of the communities. The statistical analysis showed that the average caloric value per gram total vegetation (roots, leaves, and stems) in these communities differed significantly at the 99% level ($F = 11.3$, d.f. $= 8$ and 343). The tundra estimates were considerably higher than those for the other communities indicating that communities with a long period of nonproduction accumulate a greater energy store than those which grow throughout the year. However, the pine community, with its high resin and turpentine content, also had a high energy value.

TABLE II. Average energy values for dominant species in three old-field communities collected at different seasons (Value g cal/g dry wt)

Season	Number Samples	Average Value	Coefficient Variation	Seasonal Average
January	18	4039	.152	
February	17	4225	.022	
March	3	4034	.028	4099
April	27	3900	.129	
May	24	4127	.070	
June	24	3917	.088	3981
July	21	4072	.065	
August	41	3919	.079	
September	38	4197	.061	4063
October	20	4192	.066	
November	33	4151	.097	
December	18	3907	.215	4083

TABLE III. Average energy values of dominant vegetation in ecological communities (Value g cal/g dry wt)

Community	Number Samples	Average Value	Coefficient Variation
Tropical rain-forest	15	3897	.060
Mongrove forest	11	3764	.082
Spartina marsh	14	4072	.042
Andropogon field	143	3905	.104
Herb old-field	35	4177	.096
Poa old-field	115	4075	.064
Pinus sylvestris stand	14	4787	.078
Alpine meadow	3	4711*	.005
Alpine Juncus dwarf heath	2	4790*	.003

* Bliss (pers. comm.) recently reported that the average value for tundra, based on 32 determinations, is 4709 g cal/g dry wt.

The 3 analyses described are not as precise as desired because it was necessary to compare caloric values per gram dry weight rather than values per gram ash-free weight. The large amount of ash-free weight data available for the *Andropogon virginicus* community (Table IV) shows how ash may influence the differences between categories. When the caloric values by plant part and month uncorrected for ash are compared a significant difference exists between parts at the 95% level ($F = 2.74$, d.f. $= 4$ and 32) and months at the 99% level ($F = 4.07$, d.f. $= 8$ and 32). However, the same comparison but using calories per gram ash-free weight (Table IV) shows significant differences at the 95% level between seasons only. The average value for parts for all seasons, shown below, illustrates the differences when ash is considered.

Part	*cal/g dry wt*	*cal/g ash-free wt*
Green Broomsedge	4231	4377
Standing-dead vegetation	4116	4290
Litter	3902	4139
Roots	3607	4169
Green herbs	3634	4288

ENERGY VALUES OF ANIMALS

Only limited caloric data are available for animals. Seven taxa, including invertebrates and vertebrates, are in Table V. The crabs were especially low in energy content, probably because the calcareous exoskeleton was not separated from the soft parts. E. P. Odum has provided unpublished data on the ash content of crabs from Sapelo Island, Ga., which indicate that the ash is about 51% of the total dry weight. This means that the caloric value per gram ash-free weight for crabs is about 4400 cal. The analysis of variance showed that

TABLE IV. Energy values in an *Andropogon virginicus* Old-field Community in Georgia (Value g cal/g dry organic matter)

Part	April	May	June	July	Sept.	Oct.	Nov.	Dec.	Jan.	Ave.
Green grass	4254	4372	4325	4187	4256	4529	4508	4505	4422	4373
Standing dead	4435	4338	4201	4208	4281	4205	4429	4190	4325	4290
Litter	3928	4369	4104	4225	4124	4126	4264	4029	4078	4139
Roots	4387	4056	4344	4270	4104	4074	4137	4236	3891	4167
Green herbs	4477	4157	4088	4212	4399	4429	4265	4375	4193	4288
Average	4296	4258	4212	4220	4233	4273	4321	4267	4182	4251

TABLE V. Energy values for animal taxa (Value g cal/g dry wt)

Taxa	Number Samples	Average Value	Coefficient Variation	Authority
Crustacea				
Daphnia	18	4419	.115	Richman (1958)
Stenonema	29	5596	.048	Trama (1957)
Uca and other crabs	8	2248	.188	Connell (unpubl.)
Mollusca				
Modiolus	3	4600	—	Kuenzler (unpubl.)
Insecta				
Schistocerca	8	5363	.048	Connell (unpubl.)
Annelida				
Earthworms	3	4617	.030	French *et al* (1957)
Mammalia				
Mice	8	5163	.157	Golley (1960)

the energy value of the animals, excluding the crabs, did not differ significantly ($F = 1.84$, d.f. $= 5$ and 63). In general, the values for the animals are about 1000 g cal/g dry wt higher than the plant values.

Discussion

Examination of over 600 records of plants has shown that significant differences in caloric value exist between plant parts, between vegetation collected in different months, and between vegetation growing in different ecological communities. When the variation in chemical composition of various cultivated and noncultivated crop plants reported in Morrison (1949) is considered (e.g., fat ranges from 1.0% in *Lespedeza* stems to 38.8% in wild mustard seed) and the fact that Long (1934) found that caloric values varied with light intensity, length of day, amount of nutrients, and type of soil, the observed differences are not unexpected.

Richman and Slobodkin (1960) have emphasized the constancy of the caloric value of animal tissue. Except under starvation or storage conditions animal tissue averages about 5000 g cal/g dry wt. The data in this report are less extensive but support their conclusions. Richman and Slobodkin (1960) point out that when an animal is storing food material before hibernation or a nonfeeding portion of the life cycle, the energy value of the body may increase to 6000 or 7000 g cal/g dry wt. This condition in animals is analogous to the seed stage in the life history of the plant and to the fall condition of many perennial plants which store food in the root, tuber, or rhizomes. This analogy helps to explain why significant differences exist between the plant categories.

The caloric value of a plant or animal is a function of its genetic constitution, nutritive condition, and life history. Because these factors may vary with species, seasons, and environmental conditions the ecologist making intensive measurements of energy flow through natural systems cannot depend on caloric constants or equivalents. This study shows that the ecologist must determine the energy content under the specific conditions of his particular study. However, those engaged in extensive surveys are probably justified in converting biomass to energy by using the average caloric values in the tables.

Summary

This report summarizes and evaluates the variation between caloric values of plants and animals. Analysis of over 600 records shows significant differences between plant parts, between vegetation collected in different seasons, and between vegetation from different ecological communities. Differences between animal taxa were not significant. It was concluded that ecologists should directly determine the energy content of ecological materials when studying energy flow through natural systems. It is also hoped, however, that the average values presented may be useful for energy estimation in some types of ecological research.

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INFLUENCE OF THINNING OF RED PINE PLANTATION ON SOIL[1]

F. P. Haberland and S. A. Wilde

Recent research in Germany and Russia revealed that thinnings increase the diameter of trees and hence the value of forest stands, but not the total production of dry matter. These observations are valid under many site conditions but cannot be generalized indiscriminately and interpreted to mean that the yield of the thinned stand remains the same regardless of the form of partial cutting.

A partial cutting is a major operation which returns the stagnating community of trees to a productive life by removing the unwanted members of the stand. However, if it is not performed with respect to the habitat conditions, it may result in a lasting deterioration of the site quality; it may bring about invasion of competing vegetation, depletion of soil water, increased or retarded decomposition of organic remains, loss of nutrients through leaching or biological fixation, compaction of the soil surface, rise of the water table, or accumulation of vadose water.

To counteract such adverse alterations, attempts have been made recently to detect by field and laboratory analyses the effect of cuttings on the growth factors of the treated stand, particularly on the dynamics of water and nutrients in different types of soils (Zonn 1959, Sviridov 1959). Such investigation constitutes a long overdue effort to place on a firm scientific foundation the present, totally empirical practice of silvicultural cuttings. The ultimate aim of the analytical approach is to identify the intensity of partial cuttings with the optimum subcanopy environment and thereby increase the volume and the value of the treated stand. The more restricted, immediate goal is the elimination of mistreatment of stands which diminishes the productive potential of the soil-forest entity and disrupts its biological cycle (Remezov *et al.* 1959).

This paper reports the results of an investigation of the changes in physical, chemical and microbiological properties of soil induced by heavy thinning of a dense pine plantation. Considerable time has been spent in devising analytical techniques suitable for this type of research. This report summarizes the most significant alterations observed during the last 3 growing seasons.

Methods of Study

The study was conducted in a 15-yr-old plantation of red pine, *Pinus resinosa* Ait., in central Wisconsin on a non-podzolic outwash sand of Plainfield series. The level topography, stone-free porous soil, and uniform tree growth of this 40 acre plantation were favorable for detailed investigation of the effect of thinnings on soil properties.

In the spring of 1958, ⅛ acre plots were established in a fully stocked part of the plantation, having basal area of 156 sq. ft., in a part thinned to 50% of basal area, and on adjacent cleared land (Fig. 1).

Fig. 1. General view of a part of the study area showing the clear cut plot and fully stocked plantation.

Percolation of water and movement of soluble nutrient salts were studied by alundum tension lysimeters (Cole 1958, Krause 1960). Two lysimeters were installed in each plot at a depth of 2 ft with a water column of 90 cm, approximating the tension at field capacity. The content of soil moisture was recorded by Prosser's irrometers, at 6 and 18 in. depths, Reinhart's fiberglass units, at depths of 1, 2, and 3 ft, and occasional gravimetric determinations. Recordings were made at intervals of one week, or more frequently. Precipitation data were obtained from the Griffith State Nursery, 14 miles distant.

The microbiological activity of soil was appraised on the basis of carbon dioxide evolution, measured *in situ* by 6 "spratainer" samplers and a Trico vacuum pump driven by a 6-volt storage battery (Wallis and Wilde 1957). The decomposition of surface organic matter was estimated by periodic weighings of litter, sampled by a steel frame on one foot square areas selected at random.

Air permeability was determined by a permeameter of Tanner and Wengel (1957), analyses being made 24 hrs

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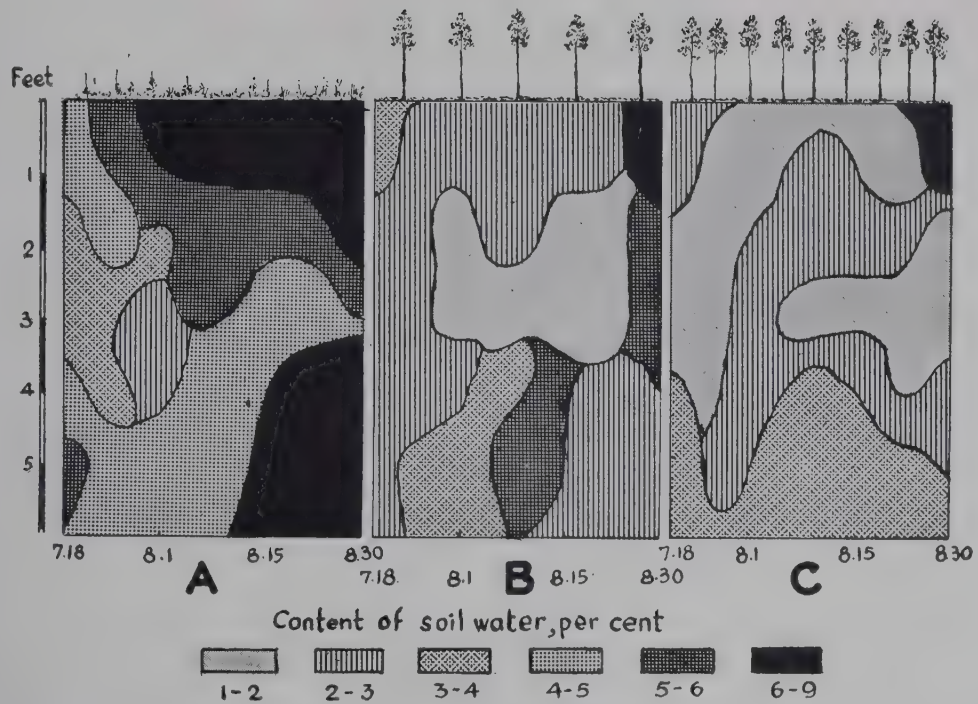

FIG. 2. Distribution of moisture during period July 18 to August 30 in soils of a cleared land (A), and a thinned (B) and a fully stocked (C) 17-year-old red pine plantation on a coarse outwash sand.

after heavy rains. The results of air permeability were related to bulk density and porosity of soils.

The chemical composition of the soil and forest litter was determined by standard procedures (Wilde and Voigt 1959). The nutrient content of lysimeter leachates was determined on 100 ml portions by a flame photometer and the phenoldisulphonic acid method. The diameter growth was recorded on average trees by ring dendrometers.

RESULTS

For 2 yrs after the thinning the downward movement of water was closely correlated with the density of the forest stand. The total volume of leachate collected from soil supporting the fully stocked plantation in the growing season of 1959 was only 290 ml, constituting 0.18 in. of rainfall. During the same period, the soil under the thinned plantation discharged 865 ml (0.54 in. of precipitation); the soil of the cutover area lost 6,385 ml (3.99 in.) equal to nearly one-half of the season's rainfall. The contents of removed NO_3, K, Ca, and Mg were closely correlated with the volume of discharged water. During the third year, however, the infiltration had undergone significant changes, undoubtedly because of the spread of crowns and root systems of the thinned stand. From June 20–September 9, 1960, the total volume of leachate under the fully stocked stand was 47 ml, under the thinned plantation 43 ml, and under the clear cut area 3,190 ml. This shows that after a short interval a thinned plantation with its increased transpiration consumes just as much water as a fully stocked stand.

The infiltration of water varied considerably depending on the intensity of rainfall. Under the reduced canopy of the thinned stand a large portion of water of light rains reached the ground and infiltrated. However, saturation of foliage and litter of the fully stocked stand by a heavy rain was followed by an unimpeded discharge. In such periods, the soil of the unthinned plantation infiltrated more water than soils of either the cleared area or partially cut stand, probably because of the higher permeability of the surface soil layer.

Gravimetric determinations of soil moisture were made at one foot depth intervals to a depth of 5 ft. Figure 2 shows the distribution of moisture from July 18–August 30, 1960, in soils of the 3 areas. These results again indicate that during the growing season there is little difference in the moisture content in soils supporting fully stocked and thinned stands even though there is a difference in the manner of water consumption. An increase in photosynthesis and transpiration of liberated trees was nearly instantly reflected in their diameter growth; within 6 wks after thinning the average increase in circumference of trees in the fully stocked stand was 0.04 in.; that of the trees in the thinned stand was 0.12 in.

The content of moisture, recorded by calibrated fiber glass units and irrometers, approximated those of gravimetric determinations. As indicated by the fluctuation of soil moisture tension, the greatest loss of water occurred in the surface layer of soil supporting the unthinned plantation. Rainfalls of less than 2 in. failed to decrease significantly the soil moisture tension at 18-in. depth which remained in soils of the fully stocked

and thinned stand at levels of 0.7 and 0.6 atm., respectively. All moisture determinations indicated that summer precipitation did not contribute to the deep storage of water in soils in any of the 3 areas.

At the end of the growing season of 1960, the average bulk density of the soil supporting the fully stocked plantation was 1.47; that of the thinned stand was 1.57, and the results were statistically highly significant. Air permeability was 12.9 cc and 10.6 cc/sec. for soils of fully stocked and thinned plantations, respectively.

During the 3 growing seasons, the weight of forest litter in the fully stocked stand remained nearly constant, averaging 11,950 lbs/acre. The weight of litter in the partially cut stand decreased to 7,800 lbs/acre.

The pattern of CO_2 evolution was strongly influenced by weather conditions. Periods of drought lowered respiration from soils of both the thinned stand and cutover area to the minimum of 2.1 g/m^2/hr. Because of the higher amount of litter and reduced loss of moisture from the surface layer, respiration most of the time was highest under the unbroken canopy, attaining in some instances the maximum level of 8 g/m^2/hr.

Analyses of the 6 in. surface soil layers revealed an appreciably lower content of organic matter and total nitrogen (1.06 and 0.036%) in the soil of the thinned stand compared with that of the fully stocked plantation (1.33 and 0.041%). Differences in the content of available nutrients and other fertility factors were within experimental error. However, there were radical differences in the content of ammonium acetate-extractible bases, especially potassium, in the litter of the unthinned and thinned plantations (K, Ca, Mg: 7.2, 0.12, and 0.04 m.e./100 g versus 3.4, 0.08, and 0.02 m.e./100 g). The impoverishment of litter should be attributed to the removal of nutrients by rains from the foliage of liberated trees and intensive leaching of litter on the ground.

Conclusions

A heavy thinning of a dense red pine plantation provided more light, water and nutrients for liberated trees. These benefits were quickly reflected in an appreciable increase in diameter growth. At the same time, the drastic reduction of the plantation density induced several unfavorable alterations in the physical and chemical composition of the coarse sandy soil. It effected a short-lasting but marked discharge of salt-bearing water from the surface 2-ft layer with subsequent removal of soluble nutrients into substratum devoid of exchange colloids. Within 3 yrs about 35% of forest litter in the thinned stand was decomposed and the soil suffered an appreciable loss of organic matter. The litter itself showed a considerable reduction in the content of exchangeable bases. The activity of microorganisms in the soil of the thinned plantation, detected by CO_2 evolution, was highly erratic, being depressed during dry spells. A slight increase in the bulk density and a decrease in air permeability of the soil supporting the thinned plantation were recorded at the end of the study.

These changes indicate that under climatic conditions of central Wisconsin, pine stands on coarse sandy soils permit only light, frequent thinnings which do not diminish the inherently low supply of soil organic matter, nutrients, and water. The reduction in the content of water available to trees of heavily thinned stands is likely to become especially pronounced upon invasion of grass and other weed vegetation. The adverse effects of heavy thinnings can be alleviated considerably by spreading the slash of removed trees on the ground.

From a methodological viewpoint, this study suggests that analytical investigations of partial cuttings must focus attention on the effects of heavy cuttings which decrease the productive potential of the soil-forest unit. This "negative approach" appears to be more fruitful than a search for an ideal degree of thinning, promising the maximum quality production. Results of investigations of heavy cuttings stress the unfavorable alterations in the habitat conditions and thus help to establish the limits in the reduction of the canopy permissible in management of different soil-forest units. For sound silviculture it is much more important to avoid a deterioration of the stand and site quality than to achieve an immediate increase in the diameter growth.

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THE ALTITUDINAL LIMITS OF VASCULAR PLANTS

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The alpine flora of the great mountain systems of the earth has attracted the interest of botanists for many years, especially since the pioneering work of Humboldt at the beginning of the 19th century. Humboldt not only collected plants at the highest altitude yet attained (on Chimborazo, in the Ecuadorian Andes) but also initiated the science of plant geography with his essays on the effect of latitude and altitude on the distribution of plants. A by-product of the mountaineering movement led by Whymper and Conway in the latter part of the 19th century was the accumulation of collections of high-alpine plants from the Andes and Himalayas. Since World War II a great many expeditions to the Himalayas and other high mountains have tremendously increased our knowledge of the plant life in some of the most inaccessible terrain on this planet.

Hemsley (1902) and Pampanini (1930) reviewed the records of the flora of the uppermost levels of the Himalayan-Tibetan region, Heilprin (1892) analyzed the flora of the Mexican volcanoes, and Fries (1905) provided a valuable discussion of high-altitude plants in the Andes. Recently, Hedberg (1951, 1957) summarized the records from the high African mountains, and Reisigl and Pitschman (1959) presented an exhaustive analysis of the high altitude flora in the Alps. The only mountainous region with a true high-alpine flora which is extremely poorly known is New Guinea; the fragmentary records are discussed by Van Steenis (1935). To my knowledge, however, no one has attempted to bring together and correlate the high-altitude records for the entire earth.

My interest in high-alpine flora developed during a Harvard Mountaineering Club expedition to the Karakoram Range, north Pakistan, in the summer of 1955. When 2 members of the climbing team, Dr. John Humphreys and Mr. Craig Merrihue, brought down 2 flowering plants from rock crevices at an altitude of over 19,000 ft, it appeared that these plants—*Draba altaica* and *Waldheimia glabra*—might represent an altitudinal record for the angiosperms. Consequently, a search through the literature was made to check on previous reports.

In the older literature Schlagintweit is credited with finding flowering plants well above 19,000 ft (up to 6038 m, or c. 19,800 ft), but as Hemsley (1902) remarked, it is probable that his altitudinal figures are erroneous. Hemsley regarded *Saussurea tridactyla,* collected in Tibet by Thorold at 19,000 ft, as the highest authenticated record; and Pampanini (1916) did not find any Himalayan plants which exceeded this level. However, very recently N. Polunin (1960) has reported not less than 9 species (not all identified) from Mohala Bhanjyang, Nepal, at an altitude of 5944 m (19,500 ft). Polunin appears to be correct in considering this as the highest altitude yet reported. He also quotes O. Polunin as having observed flowering plants as high as 21,000 ft (6400 m), but so far no specimens have been taken at such heights. At any rate, we may expect that as exploration proceeds in Nepal and other high areas in the Himalayas the present record will be exceeded and flowering plants will be found at altitudes of over 6000 m (19,685 ft).

To facilitate discussion, the data on high-alpine records has been organized into 4 tables. An attempt has been made to exert some critical scrutiny on literature reports, but this is very difficult. It is not certain that either the determinations of the plants or the altitudes stated are correct, although reports showing obvious inconsistencies have been eliminated. Undoubtedly a considerable number of reports has been overlooked, since the literature is extremely scattered. Nevertheless, the tables give a general idea of what is known about the distribution of high-level vascular plants, and at the same time suggest lacunae which need to be filled.

Table I indicates in a general way the relationship between latitude and altitudinal limits for alpine plants. As might be expected, the upper elevational limits parallel those of the tree-line (Daubenmire 1943) and snow-line, but the correlation is not exact. In some instances apparent discrepancies may simply be due to the fact that certain mountains (such as the Alps) have been more exhaustively studied. There is also reason to question the accuracy of some of the statements in the literature. Many writers speak of the upper limits for all vascular plants as though they coincided with the snow-line, but this is by no means necessarily so (Heilprin 1892, *et al.*). Furthermore, the level of the snow-line may vary several hundred feet on the same mountain. It is obvious that the relation of latitude to altitudinal limits is not simple. For instance, it is certain that vascular plants reach higher altitudes in the Mt. McKinley, Alaska, area than in the Torngat Mountains, Laborador, even though the latter are 4° farther south. As Abbe (1936) points out, the depression of the alpine flora in the Torngats is probably related to the unfavorable local climate (i.e., low temperature due to winds off the Labrador current). On the other hand, it is surprising that the upper limits for vascular plants are over 1000 m lower on the Mexican volcanoes such as Citlaltepetl (Orizaba) than they are in the Himalayas (Masherbrum), even though the latter peak is about 17° closer to the North Pole. This depression of the Mexican alpine flora relative to the Himalayan has not been explained, and is rather difficult to understand in view of the fact that in the Andes elevations comparable to the Himalayas are attained (e.g., 5800 m in Nevado de Cachi, at 25° S). Possibly this may be attributed to the effect of size of mountain masses on temperature, as suggested by Daubenmire (1947). The smaller size of the Mexican volcanic belt, according to this view, would be correlated with a lower firn line than that in the Andes or Himalayas.

The available data (Table I) indicate that the highest alpine plants occur at intermediate latitudes (28-36° in the Himalayas, 16-25° in the Andes) whereas at lower latitudes—as in the African mountains—altitudinal limits are somewhat depressed. This apparent difference may not be significant, however, because there are not enough records and it is not certain that many of these reflect the true limits. The region which best shows the latitudinal effect is the Andes, and it is still rather poorly known. The addition of alpine records from such mountains as Santa Marta (11° N), Huascarán (9° S), and

TABLE I. Relation of altitudinal limits to latitude

Locality	Latitude	Altitudinal limit* meters	Highest species	Reference
Mt. McKinley	63° N	2135	*Saxifraga oppositifolia*	Briggs (1953)
Torngat Mts.	59° N	>1340	*Luzula confusa* et al.	Abbe (1936)
Mt. Rainier	47° N	3350	*Smelovskia ovalis*	St. John & Warren (1937)
Matterhorn	46° N	4200	*Aretia alpina*	Reisigl & Pitschmann (1959)
Mt. Shasta	41° 30′ N	3960	*Draba breweri*	Harshberger (1911)
Pikes Peak	39° N	4265	*Oreoxis humilis*	Soth (1911)
Mt. Whitney	37° N	4175	*Hulsea algida*	Smiley (1921)
Masherbrum	36° N	5850	*Waldheimia glabra*	This paper
Mt. Everest	28° N	5485+	*Primula younghusbandiana*	Balfour (1922)
Citlaltepetl	19° N	4570	*Castilleja tolucensis*	Heilprin (1892)
Mt. Kenya	0°	5030	*Helichrysum* sp.	Fries & Fries (1948)
Ruwenzori	0°	5090	*Poa ruwenzoriensis*	Hedberg (1957)
Chimborazo	2° S	5200	*Senecio hallii*	Fries (1905)
Kilimanjaro	3° S	5000	*Festuca kilimanjarica* et al.	Hedberg (1957)
Sorata	16° S	5700	*Malvastrum flabellatum* et al.	Hemsley & Pearson (1901)
Nevado Chañi	24° S	5700	*Malvastrum obcuneatum* et al.	Fries (1905)
Nevado Cachi	25° S	5800	*Draba mandoniana*	Fries (1905)
Aconcagua	33° S	4115	*Acaena laevigata*	Fries (1905)
Maipo	34° S	4000	*Oxalis* sp.	Fries (1905)
Chillan	37° S	2200	*Caltha andicola* et al.	Fries (1905)
Mt. Cook	43° 30′ S	2700+	*Ranunculus grahamii*	Cockayne (1928)
Ushuaia	55° S	1290	*Empetrum rubrum* et al.	Fries (1905)

* Altitudes, as converted from feet to meters, have been rounded off to avoid giving a misleading impression of exactness (some of the records being only approximations to begin with). Latitudes have been mostly taken to the nearest degree

Vilconota (14-15° S) might clarify this puzzling situation.

Species of vascular plants which have been found at altitudes in excess of 5500 m (18,045 ft) are listed in Table II. Pampanini (1930: 276-277) has cited 54 species in the Karakoram range at altitudes of 5400 m (17,715 ft) and over; only 6 of these, however, attain 5500 m. Genera in this 5400 m group (in addition to ones cited in the tables) include: *Androsace, Braya, Carex, Delphinium, Dracocephalum, Gentiana, Leontopodium, Lloydia, Melandrium, Myricaria, Nepeta, Oxytropis, Parrya, Polygonum, Sedum,* and *Taraxacum.* The genera best represented in the Karakoram high-alpine flora are *Saussurea* and *Potentilla,* each with 5 species. As exploration of the high peaks in Asia and South America progresses, the list of species surpassing 5400 m will probably exceed 100.

It is notable that not all of these high-alpine angiosperms are arctic types. It is true that all 4 genera photographed by Polunin at 19,500 ft (*Arenaria, Lagotis, Pedicularis,* and *Potentilla*) have arctic representatives, and that the species of *Lagotis* (*L. glauca*) is the same as occurs in the arctic. *Draba* and *Saussurea,* which are conspicuous in the high-alpine flora of the Himalayas (and the former in the Andes as well), are well represented in the arctic, but the species there are not the

TABLE II. High-altitude angiosperms (above 5500 m); only plants determined to species are included

Altitude meters	Species	Locality	Reference
5945	*Lagotis glauca*	Mohala Bhanjyang, Nepal	Polunin (1960)
5945	*Potentilla saundersiana*	(same)	Polunin (1960)
5850	*Draba altaica*	Hushe Valley, Kashmir	This paper
5850	*Waldheimia glabra*	Hushe Valley, Kashmir	This paper
5800	*Draba mandoniana*	Nevado Cachi, Andes	Fries (1905)
5790	*Potentilla sericea*	Karakoram Range	Pampanini (1930)
5790	*Saussurea tridactyla*	Tibet	Hemsley (1902)
5700	*Deyeuxia glacialis*	Sorata, Bolivia	Hemsley & Pearson (1901)
5700	*Hexaptera cuneata*	Nevado de Chañi	Fries (1905)
5700	*Malvastrum flabellatum*	Sorata, Bolivia	Hemsley & Pearson (1901)
5700	*Malvastrum obcuneatum*	Nevado de Chañi	Fries (1905)
5640	*Cremanthodium nanum*	Himalayas	Good (1929)
5640	*Thermopsis inflata*	Tibet	Hemsley (1902)
5640	*Waldheimia tridactylites*	Karakoram Range	Stewart (1869)
5575	*Delphinium brunonianum*	Lanak La, Ladak	Stewart (1869)
5575	*Marrubium lanatum*	Lanak La, Ladak	Stewart (1869)
5575	*Urtica hyperborea*	Lanak La, Ladak	Stewart (1869)
5500	*Braya oxycarpa*	Karakoram Range	Pampanini (1930)
5500	*Paraquilegia anemonoides**	Gasherbrum, Kashmir	Pampanini (1930)
5500	*Pycnoplinthus uniflora*	Baltoro, Kashmir	Pampanini (1930)

* Listed as *Isopyrum grandiflorum* by Pampanini.

same as the Himalayan ones. On the other hand, such genera as *Malvastrum, Thermopsis,* and *Waldheimia* do not occur in the Arctic, as that region is defined by Polunin (1959). *Malvastrum* includes some strictly tropical species, and it is quite surprising therefore to find it represented by 2 different species in the high-alpine flora of the Andes. Thus it is apparent that while taxa of arctic affinity are conspicuous in high-alpine vegetation, they are mingled with species derived from lower elevations in the regional flora.

The Karakoram range provides the altitudinal record for the gymnosperms as well as for the angiosperms (Table III). Pampanini (1930: 69) cited *Ephedra gerardiana* var. *wallichii* from the Cipciak Valley at an altitude of 5250-5450 m (17,220-17,880 ft). It is not certain that the collection actually came from as high an altitude as 5450 m, but even the lower figure would represent the loftiest height attained by a gymnosperm. Unfortunately there is considerable confusion with regard to the taxonomic identity of the Himalayan ephedras; the plant cited may actually represent the depauperate species *E. regeliana* Florin. Further investigation is needed to establish both the identity and exact altitude of the highest species of *Ephedra.*

The highest record for a true conifer appears also to come from the Karakoram range, where Calciati (1914) recorded *Juniperus pseudosabina* F. & M, from a height of 5000 m (16,400 ft). Here again there is some uncertainty as to the specific identity of the plant; this can probably be resolved only by a careful revision of the Asiatic junipers. No gymnospermous genera other than *Ephedra* and *Juniperus* appear to reach as high as 4500 m; in fact, only 2 other genera (*Abies* and *Pinus*) appear to exceed 4000 m. The highest conifer reported in the New World appears to be *Pinus hartwegii,* which according to Heilprin (1892) exceeds 14,000 ft (4270 m) on the Sierra Negra, near Orizaba. However, Martinez (1948, 1953) credits this species with an altitude of only 3800 m (12,465 ft) and quotes no Mexican conifer at more than the 4200 m (13,780 ft) attained by *Juniperus monticola.* Martinez' citation of *Juniperus standleyi* from 4602 m (15,180 ft) on Tacaná, Chiapas, is either an error or a misprint, as the summit of that mountain is under 14,000 ft. Ochotereña (1945) reports that *Juniperus tetragona* [=*J. monticola*] reaches 4400 m (14,435 ft), but there appears to be no documentation of this statement. These conflicting reports obviously need to be clarified before the altitudinal records of New World gymnosperms can be established.

Information on high-altitude pteriodophytes (Table IV) is difficult to obtain because of the wide dispersion of the literature. The highest record is provided by Dr. R. R. Stewart (in litt.), who cites collections of *Cystopteris fragilis* by Koelz from the Chang La, Ladak, at 18,000 ft (5485 m). It is interesting that *Cystopteris fragilis,* which attains 4750 m (15,675 ft) on Kilimanjaro (Hedberg 1957), is the highest pteriodphyte of the African as well as the Asian high mountains. One of the most remarkable pteridophyte altitude records is certainly that of *Stylites andicola* by Amstutz (1957), which was at the same time a new genus of Isoetaceae and (at 4750 m) one of the highest pteridophytes ever collected. Other pteridophyte records have doubtless been overlooked, but it is probable that *Cystopteris* will never be dethroned from its position as the hardiest of alpine ferns.

The arctic and sub-arctic element in high-altitude gymnosperms and pteridophytes is even less marked than it is in the flowering plants. *Cystopteris fragilis* is the only species common to the arctic and high-alpine regions, and it is not yet certain that the populations from these areas are specifically identical. *Equisetum,* which with 7 species is the largest arctic pteridophyte genus (Polunin 1959), is not represented at highest altitudes; in the Karakoram it does not appear to exceed 12,000 ft. The junipers in the Himalayas and in Mexico which extend above 4000 m are species which are not closely related to the arctic *J. communis;* a variety of the latter does enter the extreme western end of the Himalayas but attains only 3500 m in the Hindu-Kush (Wendelbo 1952).

Until additional exploration of high peaks in America and Asia is carried out, it would be premature to attempt generalizations about the flora of the greatest altitudes.

TABLE III. High-altitude gymnosperms (above 4000 m)

Altitude meters	Species	Locality	Reference
5450	*Ephedra gerardiana*	Cipciak, Kashmir	Pampanini (1930)
5000	*Juniperus pseudosabina*	Hushe Valley, Kashmir	Calciati (1914)
4570	*Juniperus foetidissima*	Spiti, Himalayas	Heilprin (1892)
4300	*Abies* sp.	Tsela Dzong, Tibet	Marquand (1929)
c. 4265	*Pinus hartwegii*	Sierra Negra, Mexico	Heilprin (1892)
4200	*Juniperus monticola**	Cofre de Perote, Mexico	Martinez (1953)

* Attaining 4400 m according to Ochoterena (1945).

TABLE IV. High-altitude pteridophytes (above 4500 m)

Altitude meters	Species	Locality	Reference
5485	*Cystopteris fragilis*	Chang La, Ladak	Stewart (in litt.)
5030	*Polypodium hastatum*	Goring Valley, Tibet	Hemsley (1902)
4750	*Stylites andicola*	Casapalca, Peru	Amstutz (1957)
4600	*Lycopodium saururus*	Mt. Kenya	Hedberg (1957)
4570	*Polystichum lachenense*	Gilgit, Kashmir	Stewart (1944)

Many interesting problems await explanation, e.g., the observation of Heilprin (1892) that although firs (*Abies*) extend to higher latitudes and usually to higher altitudes in the Appalachians and Rocky Mountains than pines, in Mexico the situation is reversed. The apparent failure of flowering plants to reach higher altitudes on the peaks nearest the equator also merits attention. The fact that the altitudinal limits of flowering plants are sporadic and often cross the snow-line makes it difficult to establish which environmental factors are limiting, although it appears that it is most often the water supply. In the lack of a continuous vegetational cover or well-defined plant communities, the high alpine situations are analogous to the extreme deserts of Peru, Arabia, or the Antarctic continent. The most interesting result of studies on the flora of the highest summits on the earth's mountain ranges is perhaps in demonstrating the ability of plants to survive in highly adverse environments.

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A NOTE ON SILICONE OIL AS A MOUNTING MEDIUM FOR FOSSIL AND MODERN POLLEN

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Recently Andersen (1960) has critically evaluated the characteristics of a number of mounting media for fossil and modern pollen and has suggested silicone oil as the most favorable. As this represents an important contribution to pollen analytical technique, it seems appropriate to call the attention of North American workers to Andersen's paper and to mention a few facts regarding the use of silicone oil. As Andersen points out, the advantages of this medium over those previously employed are several: its refractive index is lower (1.403), it is available in a wide range of viscosities, it is non-volatile, it is chemically pure and stable, and pollen grains mounted in it do not swell as in glycerine and glycerine-jelly (a fact that is of profound importance in size-frequency studies of fossil and modern material). Furthermore, the medium can be obtained readily. Andersen has suggested that the optimum viscosity for general use is AK 2000 on the scale employed by Wacker Chemie in Munich.

Silicone oil is available in the United States from the Dow Corning Corporation, Midland, Michigan. The oils are marketed under the name of "Dow Corning 200 Fluids" and are available in viscosities ranging from 0.65-2,500,000 centistokes (cs.). AK 2000 is equivalent to 2000 cs. The standard viscosities sold by Dow Corning do not include 2000 cs, but this can be obtained by blending the 1000 and 12,500 cs oils.

It is worth emphasizing that critical grains can be relocated even after considerable time, vertical storage of slides, and moving about of slide boxes, provided that, as Andersen notes, certain precautions are taken. The pollen should not be too dense in the preparation (an undesirable characteristic in any preparation regardless of the medium used) and the drop of material used should be just sufficient for the oil to reach the edges of the cover slip. I recorded the stage coordinates of a number of critical grains which were mounted in AK 2000 oil while working at the Paleobotanical laboratories of the Geological Survey of Denmark in 1958-59. Upon completion of counts the slides were not ringed, but a drop of nail polish was placed on each corner of the cover slip to prevent movement. Ten months later, after the slides had been shipped back to the United States, the grains could be relocated at exactly the same coordinates. Hence, properly handled, silicone oil has great potential for pre-Pleistocene as well as Pleistocene material.

Movement of grains can be minimized further by employing oils of higher viscosity than Andersen has recommended. This is important in photomicrographic work in which one might wish to turn a grain to different positions and hold it while making several exposures. For example, Mrs. Clisby (personal communication) uses oil of 60,000 cs viscosity for modern material. The writer has tried this, as well as several less viscous oils, and has found silicone oil having a viscosity of 12,500 to be ideal.

The best chemical procedures for use with silicone oil are carefully described by Andersen. However, Mrs. Clisby suggests that the benzene employed must be U.S.P., thiophene free, in order to prevent the formation of a fine precipitate in the medium. My experience corroborates this.

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A FURTHER COMMENT ON THE ECOLOGY OF WOOLGRASS (*SCIRPUS CYPERINUS*)

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In a previous article (Kadlec 1958) I presented an analysis of a woolgrass, *Scirpus cyperinus* (L.) Kunth, community in Wisconsin and commented on its similarity to cattail (*Typha latifolia* L.) communities. The evidence at that time indicated that the woolgrass community developed as a result of a water level control program. Further study of the management of a Michigan waterfowl marsh by a drawdown, or temporary drainage (Kadlec 1960), indicated that this conclusion was essentially correct. In both studies the sequence of water level fluctuations was similar. The water was lowered 3 or 4 ft in May or June and held essentially stable until early fall. The dams were then closed and the marsh allowed to fill with fall rains. This schedule subjected the normally submerged soil to earlier and more severe drying than would result from a natural recession of the water levels. Under these circumstances woolgrass was a dominant plant in the Wisconsin marsh. However, the species of plants associated with it, the water depths, and the soil types were so similar to cattail communities that I suspected the dominance of woolgrass was the result of the pattern of water level fluctuation.

A more detailed study (Kadlec 1960) of a rapid drawdown of the Backus Lake impoundment in Roscommon County, Michigan, which had not been previously drained, permitted me to observe establishment of seedlings on the exposed bottoms. There cattail, woolgrass, and sedge (*Carex* spp.) seedlings soon appeared in well-defined zones around the lowered pool.

Cattail seedlings invaded only soils which remained moist throughout the summer and most new growth occurred on soils within one foot above the water level during the drawdown, indicating that proximity to the water table was important in maintaining adequate soil moisture. However, this seedling growth did not result in the establishment of new cattail stands. Reflooding inundated the shoots with at least 2 ft of water, which is greater than the depth tolerated by broad-leaved cattail (McDonald 1955). The new cattail was completely eliminated by the end of the second growing season after reflooding.

In contrast, woolgrass and sedge seedlings established themselves on exposed mudflats throughout the basin. They were most dense in the driest positions at the shallow edge of the formerly submerged area, where water depths permitted the survival of woolgrass after reflooding. The establishment of woolgrass on dry soils is a somewhat surprising characteristic for a species which normally grows in wet or aquatic situations. There are several possible reasons for this unexpected behavior. First, since the areas of maximum growth of woolgrass and sedge were exposed earliest in the season, timing alone may explain the establishment of these species on dry soils. Second, the lack of other plant growth may provide freedom from competition during seedling growth. Although both of these circumstances probably contribute, it seems likely that the tolerance of woolgrass and sedge seedlings for extremely dry conditions and the ability of woolgrass to survive reflooding are the most important factors in the establishment of woolgrass in impoundments subjected to extreme drainage in late spring or early summer.

From these observations, it is apparent that the occurrence of woolgrass as a dominant in marshes subjected to spring drainage resulted from severe drying of the soil during esablishment of seedlings. Casual observations of natural woolgrass stands further substantiate this conclusion. In most cases, woolgrass occupies low, moist areas briefly covered with water in spring. Early soil exposure to the air and (probably) rather rapid drying, provide the conditions which favor woolgrass rather than cattail. Once they are established, there is apparently little difference in the ecological status of woolgrass and cattail.

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BALANUS BALANOIDES; RECENT OBSERVATIONS ON ITS SOUTHERN LIMIT

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The report of Wells, Wells and Gray (1960) of *Balanus balanoides* several hundred miles further south than the generally accepted limits on the Western Atlantic coast is of considerable interest. They have found it to be common on wrecks on the North Carolina coast, north of Cape Hatteras but not on wrecks to the south of this point. As a result of their findings they consider that the southern limit is set by the winter sea surface temperatures *per se* as suggested by Hutchins (1947), such a limit indicating that a low temperature for re-population was the factor involved; the re-population considered by Hutchins was the production of nauplii and settlement of the cyprids giving a new generation. It has, however, been suggested that the minimum sea surface temperature of 8°C during the winter was not invariably the essential factor (Barnes 1958). In view of these new records it seems essential to stress certain features, about which there is still some misunderstanding, of the biology of *B. balanoides.*

1. It is generally agreed that the 8°C winter sea surface isotherm closely approximates to the southern limit of the species on American and European coasts.

2. *B. balanoides* would seem to be no exception to the rule stressed by Ekman (1953) that many animals are more stenothermal with regard to their reproductive behavior than with respect to other phases of their life-history. Growth and the laying down of gonadal tissue takes place at many places at relatively high temperatures, 15-20°C being fairly common (Barnes 1958); the rate of cirral beat does not fall off up to 18°C (Southward 1955); respiration of egg-lamellae is normal almost to 20°C (Barnes and Barnes 1959a); embryonic development, experimentally determined outside the mantle cavity of the adult, takes place up to 12-15°C with a normal Q_{10} for some of the stages between 5°C and these temperatures (Barnes and Barnes 1959a, Crisp 1959). On the contrary, final maturation of the gametes leading to copulation, fertilization and the formation of egg-lamellae, can be inhibited by holding animals at about 15°C for the breeding season and these processes can be induced by lowering the temperature at this time (Crisp 1957, Barnes 1958).

3. It seems reasonable in view of these facts to expect any temperature bar to the southern spread of the species to be particularly effective on the above stages of the reproductive processes.

4. At Woods Hole, where the species is common, temperatures, both sea and air, are relatively high during the summer and autumn. When the animals fertilize, sea surface temperatures are near to 15°C and Barnes (1958) therefore suggested that low air temperatures (5-10°C) prevalent at this time allowed breeding to take place in this intertidal animal. Low air or sea temperatures are "equally" effective.

5. If the deductions above are correct then an examination of the air temperatures indicated that beeding should be possible in places as far south as Charleston, S. C.

6. In the absence of records south of New Jersey it was, therefore, assumed that factors other than low winter

temperatures were ultimately setting the southern limit and the effects of competition from warm water species and the eventual deleterious effect of high summer temperatures (which have been demonstrated by Barnes and Barnes 1959b) were stressed.

The findings of Wells, Wells and Gray (1960) are in complete accord with the above hypothesis that low air temperatures are adequate to remove a temperature block, unless they find that breeding is delayed until the mid-winter months when sea temperatures have fallen to 8°C.

Further details on these southern populations would be of particular interest, both in regard to the breeding cycle and competition; it is perhaps worth pointing out that conditions on an exposed wreck where a more equable temperature regime would be expected may be somewhat different from those on a nearby shore.

Summary

In view of the recent extension of the southern limits of *Balanus balanoides* to regions as far south as Cape Hatteras, North Carolina, a discussion is given of the factors affecting the distribution of this species. It is shown that the hypothesis that either an adequate low air or sea temperature can effectively remove any temperature bar to breeding is still capable of explaining the observed distribution of this species.

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INHIBITION OF DIGITAL REGENERATION IN SALAMANDERS AND ITS USE IN MARKING INDIVIDUALS FOR FIELD STUDIES

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Toe-clipping has been widely employed in field studies for marking frogs and mammals so that they can be individually recognized. This method has also been applied to salamanders with varying degrees of success but usually is unsatisfactory for long term studies because of the tendency of the animals to regenerate lost toes.

Thornton (1949) found that beryllium nitrate inhibits the regeneration of limbs in larval *Ambystoma* which suggests that this chemical might be used for preventing regeneration of amputated toes in adult salamanders, thereby enhancing the usefulness of the toe-clipping method. The following experiment was conducted to test the feasibility of such a procedure.

Fourteen individuals of *Plethodon cinereus* (red color type) ranging in snout-anus length from 25.6 to 40.2 mm were collected near the University of Michigan Biological Station. The 3rd toe on each rear foot of every salamander was amputated with a manicuring scissors. The right foot was dipped into a solution of beryllium nitrate and held there for 1.5 minutes, after which it was rinsed with distilled water. The left foot was simply rinsed with distilled water and served as a control. The salamanders were kept on wet paper towels in individual petri dishes and maintained on a diet of fruit flies. Each one was periodically examined with a dissecting microscope during the experimental period which began on June 21, 1959, and ended on February 2, 1960.

During this period one salamander died (July 20) from an abdominal injury received during the marking, 2 were inadvertently allowed to desiccate, one escaped, and one died from undetermined causes, leaving 9 animals which were in good condition at the end of the experiment. Of these, 3 had been treated with a 0.05 N solution, four with 0.1 N, one with 0.15 N, and one with 0.2 N.

All of the control toes regenerated. Within 2 days skin was beginning to cover the wound. At the end of a month, healing was complete and the wound was covered with new skin in which pigment was beginning to appear, although elongation of the digit was not yet pronounced. At 5 months elongation was well advanced and the digits were from ⅓ to ¾ the length of the adjacent 4th toe. At the end of the experiment (slightly over 7 months) the control toes had reached approximately their original length.

It should be pointed out that these rates of regeneration are probably not typical of those occurring under field conditions as the experimental animals were kept at room temperature and thus had a higher metabolic rate during the winter than they would have had in the field.

In treated toes, the pattern of initial skin and pigment development was essentially the same as above except that in some individuals it occurred more slowly than in the untreated toes. By contrast a very marked difference between treated and untreated toes was found in the later stages of regeneration. Toes subjected to a concentration of 0.1 N or greater displayed a complete inhibition of

regeneration, and at the end of the experiment had undergone no noticeable increase in length. Variable results were obtained with those treated with a concentration of 0.05 N; in 2 salamanders regeneration occurred whereas in one it was completely inhibited. Thus, the latter concentration is too weak to produce consistent results and therefore not well suited for use in field studies.

Although beryllium has been known to cause edema and even death (Thornton *op. cit.*), the single death resulting from unknown causes in the present study is not believed to be attributable to the beryllium treatment as the animal was subjected to a concentration of only 0.05 N (the lowest one used). Animals treated with higher concentrations did not show any ill effects. However, in field studies it would be advisable to use the lowest concentration effectively preventing regeneration (in this species, 0.1 N), thereby minimizing possible undesirable effects caused by high concentrations.

A suggested procedure for field work is to carry a block of wood with holes bored in it to accommodate a vial of beryllium nitrate and several vials of water for rinsing off excess chemical after treatment. The block provides a firm support and prevents spillage caused by movements of the salamanders' feet. Treatment is also facilitated if the vials have sufficiently small mouths that undue movement of a salamander's foot is prevented while it is immersed in the solution.

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ON BIRD SPECIES DIVERSITY

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It is common experience that more species of birds breed in a mixed wood than in a field of comparable size. It is also well known that tropical forests seem to support more species than their temperate counterparts. These facts are often explained in terms of the number of "niches" or "ways of life" which the habitat provides. In this paper, a somewhat more precise analysis is attempted.

The actual number of species is better replaced by a number called the "bird species diversity," calculated as follows: Let p_i be the proportion of all of the bird individuals which belong to the i^{th} species. Then the bird species diversity, is $-\sum_i p_i \log_e p_i$. This is a formula used by communication engineers to calculate the information generated, *e.g.*, by a typist who uses the different keys with frequencies p_i. Thus, for instance, a one species community always has zero diversity; 2 species, one with 99 individuals and one with 1 individual, will have diversity of $-.99 \log_e .99 - .01 \log_e .01 = .046 + .010 = .056$ (close to zero), while 2 species each with 50 individuals will have diversity of $.347 + .347 = .694$. This illustrates why diversity is a better measure than actual number of species, for the community with 99 of one and 1 of the other seems closer to the community with one species. Margalef (1957) has frequently used a similar measure in his plankton studies. In terms of this, the question becomes: "What is it about the environment which controls the bird species diversity?"

One more refinement of the general problem is necessary. For, even if all the bird species were equally abundant, a bird census of a small area (say an acre) would have only a few of the species. Since an acre supports 3 or 4 pairs of birds, not more than 3 or 4 species could be expected to have nests in the given acre. And if the area is so homogeneous that adjacent 1 acre (say) territories are occupied by the same 3 or 4 species, then the whole area cannot have more than 3 or 4 species. This is contradicted by the abundant evidence that stands of vegetation with the degree of homogeneity resulting from a uniform history of cutting and other interference have very many (up to 106 at least in Mexico—Davis (1955)) species of breeding birds. Therefore, of course, the territories of most species are scattered rather sparsely over the area and the territories of very few species form a mosaic. It must be concluded that either the species are scattered randomly over the habitat, or else, more plausibly, that birds use some farily subtle differences in local habitat as criteria for habitat selection. Returning to the bird species diversity, it clearly can increase as the area increases. Since there is no adequate theory of "species-area" or "diversity-area" curves, all censuses must cover approximately the same area so that variations in the bird species diversity reflect differences in habitat composition rather than variations in size of census area. Although many of the censuses reported here were taken over larger areas, the breeding bird populations of a randomly chosen 5 acres of each will be compared.

The procedure of the research described here was to census a wide variety of habitats, differing in (1) plant species composition, (2) foliage height profiles, and (3) latitude, and to determine how much each of these factors influenced the bird diversity.

Measurements

Plant species composition was measured by an index of plant species diversity computed with the formula used for bird species diversity. p_i now refers to the total area of the leaves of the i^{th} plant species, expressed as a proportion of the total leaf area of all of the species on the census plot. It would be a formidable job to measure areas of individual leaves, but fortunately a much easier and more accurate method bypasses this: Imagine all the leaves lying on the ground as in the autumn. If there are, on the average 4 layers of leaves on the ground, then there are 4 acres of leaf per acre of this habitat, and if we were to push a sticky needle through the fallen leaves at random points, then an average of 4 leaves would adhere to it. And the areas of the leaves are automatically taken into consideration so that if ¼ of the leaves picked up were of some large leafed species, it would indicate precisely the

same total leaf area of that species as of a small leafed species whose leaves were picked up with the same frequency. Rather than wait for the leaves to fall, it is easier to erect a stiff wire and count the leaves it touches (since leaves on trees do not lie horizontally, some error is introduced in this way, but it gives a convenient approximation). For the canopy, rather than using a wire, a sighting was made vertically through a 10 foot aluminum pipe of 1¼ inch diameter and the number of leaves which a wire would intersect was estimated.

For coniferous trees, and sometimes for deciduous, it seems preferable to use fraction X of sky not obscured by foliage and estimate the number n of leaves which a wire would intersect by the formula $e^{-n} = X$ which is the first term of the Poisson distribution.

Thus, if 90% of the sky is obscured by foliage a fraction equal to $\frac{1}{10}$ is unobscured and since $e^{-2.3} = \frac{1}{10}$, this is equivalent to an average of 2.3 randomly placed leaves (of any size!) above the point from which observation was made. In future measurements vertical photographs analyzed by a recording microdensitometer will be substituted for the more subjective estimates of percentage. Since leaves may not not be randomly placed this is obviously only an approximation, but in practice it seems quite accurate.

From the foliage height profiles a number called the foliage height diversity was calculated using the same formula $(-\sum_i p_i \log_e p_i)$ as before. In this case p_i is the proportion of the total foliage which lies in the i^{th} of the chosen horizontal layers. The profiles were constructed as follows: At a sequence of heights above the ground a white board, marked in squares, was moved horizontally away from an observer at the same height until ½ of its surface was obscured by leaves from the observer's view. In forests, the board atop a high pole was erected at trial distances from the observer until an acceptable one was found. The distance D between the observer and the board was then measured and the foliage density k at that height was estimated

$$\text{from } e^{-kD} = \tfrac{1}{2} \text{ or } k = \log_e 2/D.$$

This formula too is only approximate, but seemed satisfactory. Roughly it is derived as follows. The area of leaf silhouetted against the board will be nA, say, where A is the area of the board and n is the leaf silhouette per unit of board area. The volume of space in which these leaves lie is DA, so the leaf silhouette area per unit of volume of space is

$$\frac{nA}{DA} = \frac{n}{D} = k.$$

As before, n can be estimated by the first term of a Poisson distribution so that $e^{-n} = \frac{1}{2}$ or $n = \log_e 2$. The method assumes that the proportion of leaf area which is similar in all 3 layers. The size of the board is thus unimportant (since the A's cancel out) except that a large board gives an average over more vegetation (10″ × 18″ was used inm ost of this work). In each plot, at least 16 such measurements were averaged at each of the following heights above the ground: 6″, 2′, 5′, 10′, 20′, 30′, 45′, 60′. A profile of foliage density was drawn by eye passing through each of these calculated points. The profiles of the primarily deciduous areas censused are shown in Figure 1. (The Florida

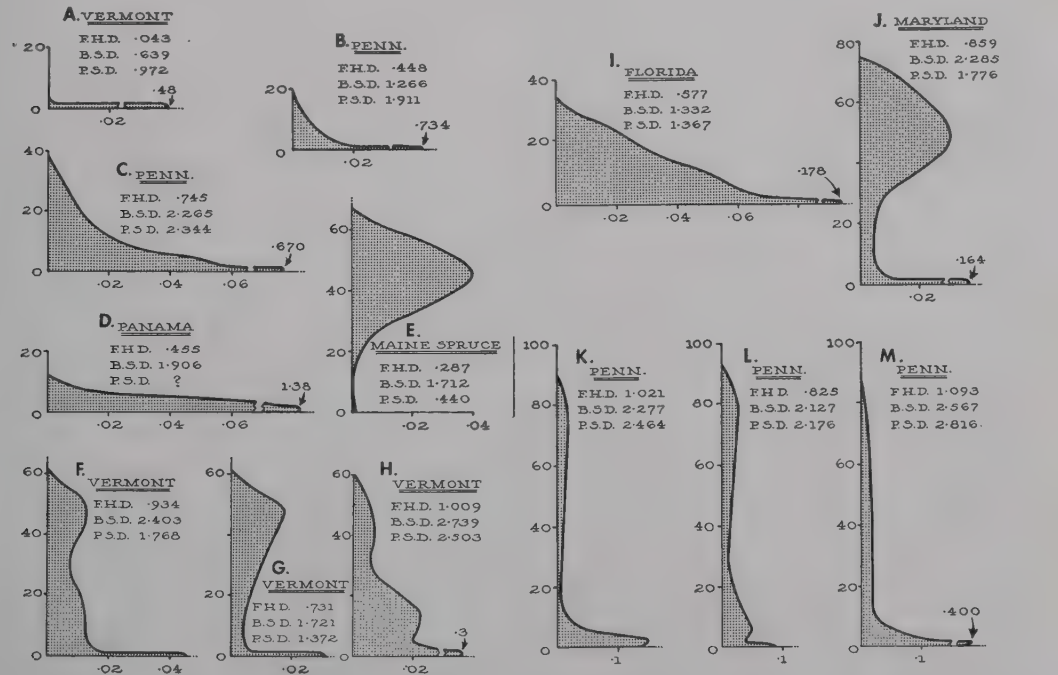

FIG. 1. The densities of foliage (measured in square feet of leaf silhouette per cubic foot of space) are plotted along the abscissae. The height in feet above the ground is the ordinate. F.H.D. is foliage height diversity, B.S.D. is bird species diversity, and P.S.D. is plant species diversity.

bird census was taken by Wolfenden *et al.* 1959, who kindly allowed measurements to be made in this area). The area of the profiles is divided into 3 horizontal layers and the proportions of the whole that each constitutes is the p_i used in the formula.

Results

The actual censuses are in Table I, in which the number of territories, or fraction of territories, is entered.

The layers 0′-2′, 2′-25′ and over 25′ are marked on the profiles in Fig. 1 and the corresponding foliage height diversity and bird species diversities are shown as well as plant species diversity and latitude. These are plotted as a graph in Figure 2, showing a close fit to the line:

$$\text{bird species diversity} = 2.01 \text{ foliage height diversity} + .46,$$

calculated by least squares. Various other subdivisions of the profile into horizontal layers were tried, and the layers 0-2′, 2′-25′ and $>25'$ were chosen as those layers which made the collection of points on the graph most orderly. It is of interest that this subdivision was chosen after the Vermont censuses were taken in 1959 and that it continued to be appropriate for the censuses in 1960, elsewhere. Such subdivisions as 0-3′, 3-30′ and $>30'$ were nearly as good, but more nearly equal subdivision (*e.g.* 0-15′, 15′-30′, $>30'$) made a very scattered

Table I. Numbers of breeding bird territories per 5 acres for the regions shown in Fig. 1

	A	B	C	E	F	G	H	I	J	K	L	M
mourning dove												1
yellow billed cuckoo									.5			
r. t. hummingbird					.5							.5
flicker			1							1		.5
red-bellied wood pecker									.5			
yellow-bellied sapsucker							1					
hairy woodpecker						1	.5					
downy woodpecker										1		
crested flycatcher								1	1		1	
acadian flycatcher									1.5			
wood pewee										2	2	1
olivesided flycatcher							1.5					
blue jay										1	1	.5
black-capped chickadee					1		.5					
tufted titmouse									1.5	1.5	1	1
white-breasted nuthatch						1					1	
brown creeper					1							
winter wren							1					
catbird			1							1		1
robin					.5		.5					
wood thrush										1	1.25	
olive-backed thrush						2						
veery thrush							1					
gnatcatcher								1				
golden-crowned kinglet					1							
white-eyed vireo									1			
yellow-throated vireo								1				
red-eyed vireo					1	3	1		2.5	2	4	1
black and white warbler							.5					
prothonotary warbler									2			
blue-winged warbler			.5									
Nashville warbler							1					
parula warbler									1			
magnolia warbler				.5	1.5		1.5					
black-throated blue warbler						1						
myrtle warbler				2			5					
black-throated green warbler				5	1							
blackburnian warbler				1	2	1						
bay-breasted warbler				3								
prairie warbler			2									
ovenbird					1.5					3	3	
Kentucky warbler									1	1	1	.5
mourning warbler							.75					
yellowthroat		1	2.5				3					2
yellow-breasted chat			2									
Canada warbler							2					
redstart				1	1.5				2			
grackle												1.5
scarlet tanager							.5					
summer tanager								2				
cardinal			1							1		1
indigo bunting			1.5									1.5
goldfinch	1	.5										
towhee		.25	1.5				1				1	1
slate-colored junco					.5							
field sparrow	2	1	3									
white throated sparrow							1					
song sparrow			.5									1

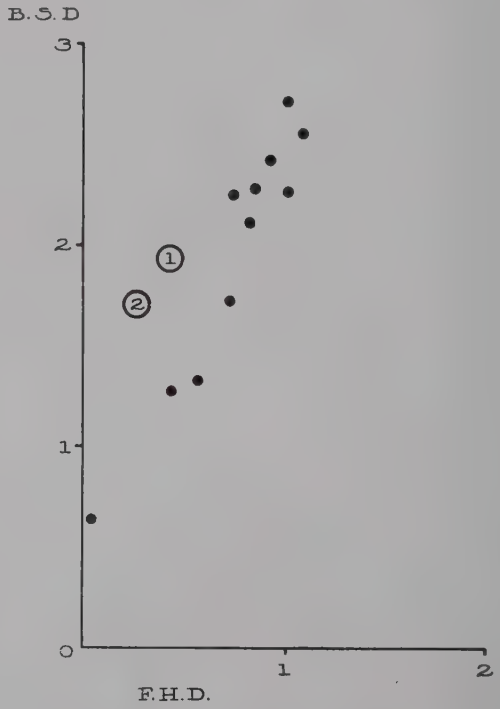

Fig. 2. Bird species diversity is plotted against the foliage height diversity of deciduous forest plots. Point 1. is census D of tropical savannah and point 2 is census E of pure spruce forest.

graph. The linearity of the cluster of points indicates that the addition of a new layer of a given amount of foliage results in the same increase in bird species diversity, (not however the same increase in number of bird species) no matter which layer (0-2′, 2-25′ or $>25'$) is added, and no matter which other layers are present to begin with. Thus, we can say that the layers 0-2′, 2′-25′ and $>25'$ are roughly equally important to the birds. (The reasons for this will be discussed later.) Looked at from this point of view, we can see the trouble with the other subdivisions. For definiteness, consider 0-15′, 15′-30′, $>30'$. Adding a 0-15′ layer to a habitat without it causes a much greater increase in bird species diversity

than the addition of the layer $>30'$. There is nothing biological about the number of layers chosen. Four or 5 layers in a roughly similar subdivision would be more cumbersome to analyse but would presumably be even more accurate. In particular, the layers 0-½′, ½′-6′, 6′-15′ and $>15'$ suggested by Elton and Miller (1954) allow a rather good prediction of the bird species diversity.

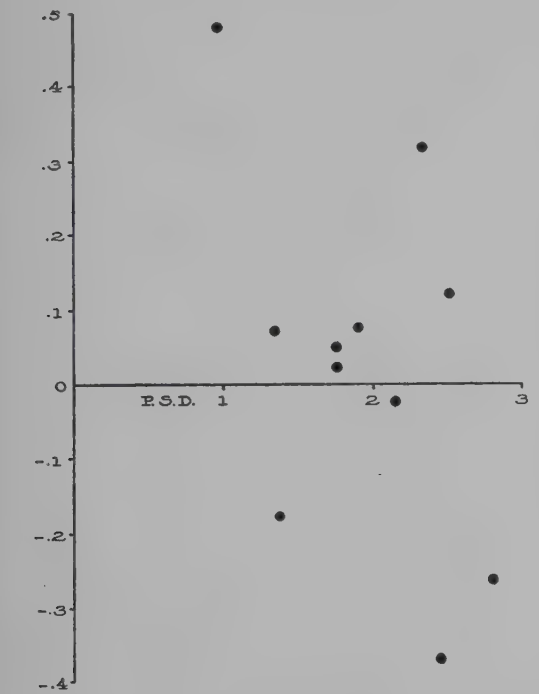

FIG. 3. The ordinate is the residual scatter, after partial regression of bird species diversity on foliage height diversity. This is plotted against plant species diversity, showing that knowledge of plant species diversity does not provide additional knowledge of bird species diversity. The least squares equation was B.S.D. = 2.546 F.H.D. — .152 P.S.D. — .250, and the residual scatter was computed from the formula B.S.D. — 2.546 F.H.D. — .048.

The next question is: How much of the remaining scatter, *i.e.* how much of the variability in bird species diversity not accounted for by the variation in foliage height diversity, can be accounted for in variations of plant species diversity and latitude? Remarkably enough, the answer is "None." This is seen most easily by glancing at Figure 3 which shows that the residual scatter after partial regression is more or less independent of plant species diversity. Thus, although plant species diversity alone is a good predictor of bird species diversity it is because plant species diversity is high when foliage height diversity is high, and, when this is taken account of, plant species diversity can contribute nothing further. In other words, habitats of the same profile have the same bird species diversity whether composed of few or many plant species. As a striking example of this, the almost pure stand of white spruce on Mount Desert Island in Maine which the authors studied earlier (MacArthur 1957) had as great a bird species diversity as the forests of very mixed composition in Pennsylvania and Maryland.

The lack of effect of latitude is puzzling but is only tentative since a rather poor sample of latitudes have been examined. Furthermore, a brief trip to Panama yielded a tentative bird species diversity in a savannah area of 1.906 and foliage height diversity of .455 (see Fig. 2). Thus, the tropical bird species diversity is much greater than the temperate one for habitats of comparable profile. The excess of tropical savannah over temperate fields is about equal to the excess of the bird species diversity in the tropical forest over temperate forests. These facts will be discussed further in a separate paper.

DISCUSSION

These results are rather statistical in nature. What is their meaning in terms of individual birds or species? The simplest explanation which seems to account for the observations, describes the "shape" of a bird's niche. Let us return to the picture of many territories distributed over an area and consider the following evolutionary argument. A large number of species can be accommodated in an environment in a variety of ways of which there are 2 extremes. Each species may have different habitat preference and feed throughout this habitat on all kinds of food, or, all species may share the entire habitat, each species feeding on a different variety of food or in a different situation within the habitat. The first extreme violates what might be called the "jack of all trades—master of none" principle that natural selection favors the increased efficiency resulting from a certain amount of specialization. In the other extreme, specialization has proceeded so far that time and energy are wasted in travelling between spots for which the specializations are adapted. It is hard to say just where the balance of these opposing requirements would be reached, but it is clear that greater specialization resulting in increased efficiency would always be favored as long as no time or energy are wasted. And no time or energy will be wasted if niches are "convex" in the sense that between any 2 fairly distant feeding places there will be a fairly natural route also consisting of feeding places. A specialization to a single tree species in a mixed forest would clearly violate this since, in passing from one suitable tree to another, the bird would go through many unsuitable ones. Thus, natural selection would tend to eliminate a situation in which bird species diversity depended upon tree species diversity, unless, as in some fruit eating species, a very remarkable improvement in efficiency is achieved along with the restriction in feeding position. Thus, one principal result of these censuses can be predicted on assuming that niches are convex.

Next, we may ask "why are the layers 0-2′, 2-25′, $>25'$ equally important? Is it because birds respond to different heights, or is it because they respond to different configurations of vegetation in different layers?" In the latter case, herbs, bushes and trees presumably correspond to the layers 0-2′, 2-25′ and $>25'$ respectively, although small trees count as bushes etc. There is good evidence for this latter explanation. For, although deciduous forests vary principally with height above the ground and hence have a bird diversity predictable from the height profile, conifers (especially spruce) have a marked "inside" and "outside" for which

species are specialized (MacArthur 1957). Hence bird species diversity would be high in a mature spruce forest even if few layers were present. This is precisely what happens in the Maine white spruce wood mentioned earlier, with bird species diversity of 1.712 and foliage height diversity of .287 which is seriously off the graph of deciduous forests (Fig. 1).

A different way of looking at the data gives additional insight. Watt (1947) has pointed out that plants are distributed in patches. Hutchinson and MacArthur (1959) attempted to explain the sizes of coexisting organisms in terms of an environment composed of a mosaic of kinds of patches. Different combinations of patches formed the habitats selected by different species. The present research can be easily interpreted in terms of this picture of the environment. In fact, our results suggest that the patches forming the birds' environmental mosaic are sections of canopy C (over 25'), patches of bushes B from 2-25', and the herbaceous and other cover H less than 2' from the ground. And the sequence of patches encountered in moving through the habitat (or in taking ever larger samples) is then represented by a sequence of letters *e.g.* C, B, H, H, B, C, ,,, with certain random properties but also subject to the condition that the long term frequency of C's, B's, and H's should conform to their respective densities (p_i) in the particular habitat. If the sequence is ergodic, which defines what we call a homogeneous habitat, then it is well known that the uncertainty of the next letters in the sequence is appropriately measured by the formula $-\sum_i p_i \log_e p_i$ which we used. If, instead of considering the uncertainty of future single letters in the sequence, we ask for the uncertainty of future pairs of letters, the formula becomes $-2\sum_i p_i \log_e p_i$ which is $2 \times$ foliage height diversity, which is essentially the predicted value of the bird species diversity. Thus we can say that bird species diversity is determined as if the birds recognized suitable habitats by pairs of foliage types ($>25'$, 2-25', 0-2'). The species area curve could then be predicted from this.

Acknowledgments

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Summary

1. Bird censuses on a wide variety of areas are compared in order to see what aspects of environmental variation control bird species diversity.
2. Indeciduous forests, bird species diversity can be predicted in terms of the height profile of foliage density. Plant species diversity, except by influencing this profile, has nothing to do with bird species diversity. The layers 0-2', 2'-25', $>25'$ seem equally important in determining bird species diversity; these layers presumably correspond to different configurations of foliage. This should not be interpreted as evidence that a forest is made up of discrete layers. These 3 layers are constructed by the observer.
3. An evolutionary argument is given which predicts the observations and at the same time suggests that niches should be "convex." Supporting evidence is provided.
4. These results provide no evidence about the real causes of tropical diversity (*i.e.* whether the temperate regions, given enough time, can support as great a diversity as the tropics now have) or about the diversity which could be expected in a composite census of 2 habitats. These are essentially different problems and are under investigation now.

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HABITAT OF JUVENILE SHRIMP (FAMILY PENAEIDAE)[1]

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For the past 50 years penaeid shrimp have been studied along the shores of the Gulf of Mexico and the South Atlantic coast of the United States. These shrimp are of intrinsic interest to zoologists. The group differs from other higher Crustacea in that the eggs are shed free into the water and develop into larval stages ranging from nauplii (very similar to early copepod developmental stages) to post-larvae, with as many as 14 probable molts intervening, the precise number still being a matter of argument. A 2nd reason for the extensive study of the Penaeidae is that the shrimp fishery is the most valuable one in the United States (*cf.* the various annual fishery

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landing statistics reported by the U. S. Fish and Wildlife Service).

The general life history of the white shrimp, *Penaeus setiferus,* has been rather laboriously worked out. Both the white shrimp and brown shrimp, *P. aztecus,* spawn in the saline waters of the Gulf and grow up in low salinity, estuarine areas of the coast. There are many indications that salinity is an important factor in the distribution of shrimp. The white shrimp is almost completely euryhaline and the young have been found in waters of 0.4 $^0/_{00}$ saline (Gunter and Shell 1958). Young brown shrimp have been found in salinities of 0.8. Table I gives comparative figures of these 2 shrimp in low salinity waters.

TABLE I. Numbers of white and brown shrimp taken in low salinity waters. Data from Gunter and Shell (1958)

Salinity Range	0.42-0.48	.75-.82	2.02-4.05
Penaeus setiferus..	2	20	326
Penaeus aztecus...	0	1	52

Apparently, white shrimp have a greater tolerance of low salinities than brown shrimp. Correspondingly, the greatest production of white shrimp has always been from the vast estuarine area of the Louisiana coast, since the early days of the fishery, and the greater brown shrimp production has come from the drier Texas coast. The latest figures (Gunter in press) are dependent upon recently improved statistical collections by the U. S. Fish and Wildlife Service. They show that for the 4-year period 1956 to 1959, the average annual production of headed white shrimp for Louisiana and Texas was 13,335,000 and 4,641,000 pounds respectively. Brown shrimp production for the same 2 states was 11,928,000 and 39,104,000 pounds, respectively. Differential production of these 2 species of shrimp is also found along 4 areas of the Texas coast in correspondence with higher and lower salinity regimes of the bays. The data are presented elsewhere (Gunter in press) and their exposition here would prolong this account unduly.

In Texas waters there is a direct correspondence between rainfall of the State and production of white shrimp (Gunter and Hildebrand 1954). In this connection it should be noted that when the long drouth was broken in Texas in 1957 the white shrimp production jumped from an all time low of 2,229,000 pounds in 1957 to 7,370,000 pounds in 1958 (Gunter in press).

The above facts are all in agreement with the hypothesis that the salinity of Texas coastal waters are, on the whole, higher than the optimum for juvenile white shrimp, and the salinities are at an optimum in Louisiana waters, where the flow of the mighty Mississippi is a dominant environmental factor. Similarly, these facts are in agreement with the assumption that salinities of inshore Texas waters are optimum for brown shrimp production, but Louisiana waters are a bit too low. Nevertheless the optimum salinities for production and growth of these 2 species of shrimp have not been precisely determined. The writer and Mr. Percy Viosca, of Louisiana, have been concerned with field studies of white shrimp since 1931 and 1916, respectively. Our general observations indicate that the optimum salinity for juvenile white shrimp lies below 10 $^0/_{00}$. A program of the Texas Game and Fish Commission, which is now underway, should answer that question, and many others.

The usual low salinity distribution of juvenile white shrimp does not mean that they are not sometimes found in high salinity waters. Such distributions are well known to shrimp biologists. As Lindner and Anderson (1956) have noted, such small shrimp are often found in high salinity waters near the lower ends of bays because they have moved in as larvae from the still higher salinity areas of the open Gulf. Small shrimp are not killed or precluded by high salinity as if it were poison; they simply do not do well in it, for reasons unknown. At present I have data from the Laguna Madre of Texas on a small population of white shrimp, numbering 115, and ranging from 15 to 66 mm in total length—all taken at a salinity of 41.3 $^0/_{00}$.

These facts and the data presented by Hoese (1960a) who found 628 white shrimp 20-83 mm long, along the Gulf beach in October, do not mean that "salinity in broad ranges is inconsequential to young shrimp," as he concluded. He did not give precise salinities, but only mentioned that they varied from 22.2 to 26.5 $^0/_{00}$ and listed salinities from "other relatively high salinity localities in the area," these being in the bays, as 19 to 26 $^0/_{00}$. Such salinities are not very high. The writer has previously listed both white and brown shrimp, 28 mm in length, at salinities above 30 $^0/_{00}$ (Gunter 1950, Figs. 2 and 4.) The fact remains that the Gulf beach is not the rearing grounds for white shrimp on the Texas coast. Instead, the shrimp mature in the bays. It is well known that shrimp leave the bays in the fall and that mixed populations are then found on the Gulf beach, as Hoese found at that time. Such findings are not new evidence and they are not newly relevant to the distribution of shrimp, as related to salinity or other factors.

There is one and only one exception, so far as I know, to the statement of M. D. Burkenroad that shrimp larvae which do not make it into the bays are in a hopeless situation. Mr. Percy Viosca, Jr. has found that the offshore waters of the Louisiana coast, near the Southwest Pass mouth of the Mississippi River, are rasing grounds for young shrimp. These waters, however, are of low salinity and are estuarine in nature, although they lie off the mainland coast in the open Gulf.

Hoese's reference to *Penaeus duorarum* as euryhaline is simply in error. The white and brown shrimp are not quite fully euryhaline and the pink shrimp, *P. duorarum,* is the only one of the 3 Gulf coast commercial species which is clearly non-euryhaline. Darnell and Williams (1956) took the pink shrimp at a salinity of 3.9 $^0/_{00}$ and Hoese (1960b) recorded it at 2.7, these being the lowest on record.

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THE RELATIVE ABUNDANCE OF SNAKE SPECIES[1]

Frederick B. Turner[2]

Introduction

There have been a number of attempts to develop empirical mathematical descriptions of relative species abundance, *e.g.* the logarithmic series (Fisher *et al.* 1943, Williams 1947); the lognormal series (Preston 1948, 1958); and the negative binomial series (Brian 1953).

Another approach is that of MacArthur (1957, 1960). In these studies MacArthur has not attempted so much to predict relative abundances as to deduce something of the organization of communities by an analysis of observed species abundances. Furthermore, MacArthur restricts himself to a consideration of what he terms "equilibrium species" (*e.g.* most birds), in which rates of increase do not fluctuate markedly and the populations are fairly stable. MacArthur (1957) used bird census data gathered by Saunders (1936) from Quaker Run Valley in New York to test the applicability of 3 hypotheses, differing in the manner in which the environment is partitioned among its occupants. He concluded that the best accord between the observed and predicted species abundance obtained when the environment is visualized as being subdivided into a number of contiguous but nonoverlapping niches—comparable to the random fragmentation of a stick. The number of fragments represents the number of species and the lengths of the fragments are proportional to the abundance of each species. This hypothesis, hereafter referred to as MacArthur's hypothesis, seems to work well for snails (*Conus*) in Hawaii (Kohn 1959) but MacArthur (1960) states that "censuses of trees, fish, soil arthropods and other organisms deviate greatly from . . . expectation . . ."

We may now inquire as to whether MacArthur's approach differs qualitatively from earlier studies. Saunders' bird data fit the lognormal distribution well (Preston 1948), and the negative binomial distribution somewhat better (Brian 1953). However, these workers were interested in predicting species abundances and not in deducing principles underlying the organization of communities. Furthermore, I cannot see how the earlier distributions can be interpreted in terms of any simple biological hypothesis.

In a comprehensive review of species abundance and community organization Hairston (1959) discusses the effect of increased environmental heterogeneity on the applicability of MacArthur's hypothesis. Both MacArthur (1960) and Hairston agree that there is an effect but, while MacArthur has shown that bird censuses depart more radically from expectations as the ecological diversity of the sampled area increases, Hairston demonstrated that for some other kinds of animals the fit is improved by greater heterogeneity. Hairston used a formula given by Barton and David (1956), and subsequently developed independently by Peter Ovenburg, to calculate the theoretical variances of census data. The theoretical variances were then compared with variances calculated from the actual data, and the ratio of these values afforded an objective expression of goodness of fit. Hairston made 2 kinds of tests. One involved lumping census data from different communities. The lumped data may logically be expected to show the effect of increased heterogeneity. The other test involved lumping a number of samples from a single community and comparing the fit based on lumped data with the average fit of the individual replicates. The idea is that a number of samples combined should reflect actual species abundance more accurately than any one alone.

Data from Snake Populations

Even this cursory review indicates the need for further information. The following data pertain to the relative abundance of snake species (which are probably equilibrium species) and are drawn from Klauber (1939) and Dunn (1949). The first paper deals with snakes collected in San Diego County, California, over a 16-year period. This collection is not free from bias, but because individuals of exceptionally abundant species were recorded (though not necessarily preserved) the major source of bias is reduced. The 2nd paper pertains to a collection from Panama, and affords the best index (with which I am familiar) of the true relative abundance of ophidian species in a large area. The reader is referred to the original paper for an interesting account of how and why this collection of almost 11,000 specimens was assembled. This collection has been analyzed in terms of the logarithmic series by Dunn and Allendoerfer (1949), who found reasonable accord with theoretical predictions.

The Panamanian collection was drawn from parts of Panama: 1232 specimens from the western states of Coclé and Herrera (Coclé); 2500 specimens from the north (Atlantic) coast, including parts of Colon and the Canal Zone (Chagres); 3914 specimens from the southern coast, including parts of the state of Panama and the Canal Zone (Sabanas); and 3044 specimens from the easternmost state of Darien (Darien). The species have been ranked in order of abundance, and logarithmic plots of numerical abundance vs. rank prepared for (1) the 4 separate Panamanian collections, (2) these collections combined, and (3) the San Diego County collection. These data are recorded as solid lines in Figure 1. The expected abundance (N) of each species in a cohort of S species, according to the postulates of MacArthur's hypothesis, has been calculated for the same groups. The resulting curves are plotted as dotted lines in Fig. 1.

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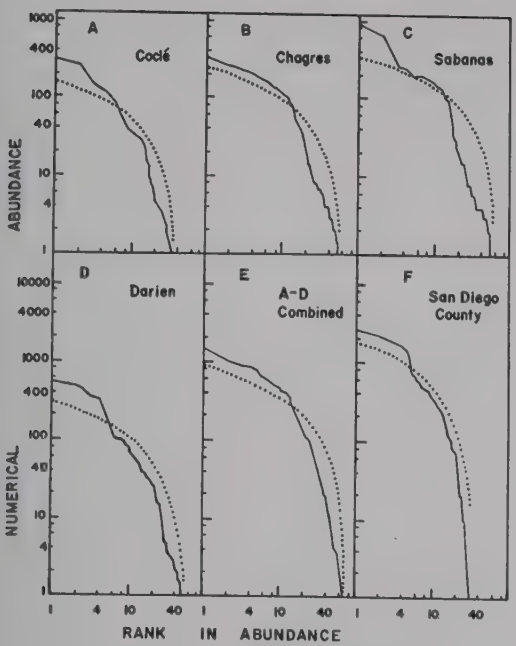

FIG. 1. Observed abundance of ophidian species (solid lines) and species abundance postulated according to MacArthur's hypothesis (dotted lines).

The formula used to calculate the theoretical values is given by Hairston (1959) as:

$$\frac{N}{S} \sum_{i=1}^{r} \frac{1}{(S-i+1)}$$

where r is the rank in rareness and i varies from 1 to S (see also MacArthur 1957).

In attempting to assay the effect of increased environmental heterogeneity both kinds of tests used by Hairston (1959) have been performed. The effect of lumping communities may be examined by comparing the variance ratio of the entire Panamanian collection and the ratios of the collections from the 4 different areas involved (Table I). Dunn (1949) gives collection data for separate years from one locality (Yavisa) in Darien and one (Agua Clara) in the Chagres area. These data may be adapted to the second type of test used by Hairston (Table I). The theoretical variances have been calculated from the formula given by Hairston (1959):

$$s^2 = \left[\frac{N^2}{S^3} \sum \left(\sum_{i=1}^{r} \frac{1}{S-i+1} \right)^2 \right] - \frac{N^2}{S^2}$$

The assistance and cooperation of Fred Stahl of the Wayne State University Computing Center, and of William Anderson of Western Data Processing Center, in programming the above formulae are gratefully acknowledged. Both Nelson Hairston and Robert MacArthur have made helpful criticism and suggestions.

DISCUSSION

The first conclusion to be drawn from the above analysis is that the observed species abundances conform reasonably well to those predicted by MacArthur's hypothesis. The departures are of the sort which so far seem to be "typical"; *i.e.*, the common species are too common and the rare species too rare. However, the variance ratios (*i.e.*, observed variance/theoretical variance) are small compared to most of those calculated by Hairston (1959).

TABLE I. Variance ratios and related data from snake censuses examined in terms of relative species abundance

Locality	Total Number of Species (S)	Total Number of Individuals (N)	Observed Variance	Theoretical Variance	Variance Ratio (observed/theoretical)
Coclé	30	1232	4126	1461.9	2.8
Chagres	53	2500	4454	2033.7	2.2
Sabanas	52	3914	24074	5171.0	4.7
Darien	44	3044	14343	4310.5	3.3
Panamanian collections combined	63	10960	76433	27993.5	2.7
San Diego Co., Calif.	26	12947	482778	211205.6	2.3
Yavisa					
1933	33	366	340	107.8	3.2
1934	35	790	1219	449.1	2.7
1935	31	587	578	312.0	1.9
1936	32	310	160	81.9	2.0
1937	31	268	196	65.0	3.0
5 yrs. lumped	40	2321	8685	3006.8	2.9
Agua Clara					
1938	35	176	20	22.3	0.9
1939	35	270	75	52.5	1.4
1940	29	239	94	58.6	1.6
1941	26	149	43	28.0	1.6
4 yrs. lumped	47	1103	1023	498.7	2.1

The Panamanian collection, drawn from 4 parts of the country, permits a study of the effect of environmental heterogeneity on the applicability of MacArthur's hypothesis. Climatically the Coclé, Sabanas, and Darien areas are similar (65-73" of rainfall), while the Chagres region has 100-129" of rainfall. There are associated floristic differences. Thus the entire Panamanian sample is drawn from a more heterogeneous area than that represented by any one of the 4 subsamples. Lumping the 4 subsamples results in a variance ratio (2.7) only slightly less than the average (3.25) of the 4 areas considered separately. However, the effect of heterogenity seems to be in the direction predicted by Hairston (*i.e.* toward a better fulfillment of random expectations), and not as MacArthur found in bird populations. The average variance ratio for the collections at Yavisa during 5 years (2.5) and 4 years at Agua Clara (1.4) are less than the variance ratios of these collections lumped (2.9 and 2.1 respectively). This result is of the same sort that Hairston (1959) obtained in his analysis of soil arthropod populations. Hairston interprets this as a demonstration of organization (and hence non-randomness) of the community.

CONCLUSIONS

The snake populations analyzed here appear to be "equilibrium populations," in that relative abundances of species conform well to MacArthur's hypothesis. The data appear to support Hairston's conception of community organization based on information theory, in that increased environmental heterogeneity does not have the effect that MacArthur has observed in bird populations.

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EFFECT OF A COVER OF DUCKWEEDS AND THE ALGA *PITHOPHORA* UPON THE DISSOLVED OXYGEN AND FREE CARBON DIOXIDE OF SMALL PONDS[1]

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Introduction

During August of 1959 the authors investigated a pronounced mortality of fishes in a 0.5 acre pond. The mortality involved bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), carp (*Cyprinus carpio*), black bullheads (*Ictalurus melas*) and grass pike (*Esox americanus*). At the time of the first observations the fishes that had not already succumbed were gasping at the surface. The pond was completely covered with duckweeds (*Wolffia columbiana* and *Lemna minor*). The dissolved oxygen under the mat of duckweeds was zero at all levels while the free carbon dioxide was 60 to 100 ppm. On the basis of these observations it was concluded that the duckweeds were responsible for the fish mortality and it was decided to investigate the dissolved oxygen and free carbon dioxide content under growths of duckweeds as well as under surface growths of the filamentous alga *Pithophora*.

Method

During August of 1959 and August and September 1960 observations were made on one pond with no cover, 3 ponds with dense growths of duckweeds and 2 with dense surface growths of *Pithophora* (Table I).

Surface water samples were taken with a Hale sampler while deeper samples were taken with a Kemmerer sampler. Dissolved oxygen was determined by the sodium azide modification of the Winkler method. Free carbon dioxide was determined by titration with sodium hydroxide to a phenolphthalien end point.

Results

The investigation of other ponds (Table I) which had a cover of duckweeds revealed the presence of dissolved oxygen and free carbon dioxide levels quite similar to that of Pond 1, *i.e.*, oxygen was very low and carbon dioxide abnormally high. The observations given in Table II indicate that a covering of duckweeds and to a lesser extent a covering of *Pithophora* can reduce the dissolved oxygen of water to a critical level for fishes. There is also an increase in free carbon dioxide. A comparison between ponds with some cover and a pond without cover (Table II) demonstrates a marked difference in these 2 variables.

Although actual fish mortality was observed only once (Pond 1, 1959) repopulation of Pond 1 by flooding occurred in the fall of 1959 and, at the time of the August 1960 observations (Table II), the fishes were gasping at

Table I. Physical description of ponds utilized in a study of the effect of a covering of duckweeds and *Pithophora* upon dissolved oxygen and free carbon dioxide

Pond No.	Acres	Average Depth (Feet)	Location	Vegetation
1	0.5	3.5	Forested ravine	*Wolffia columbiana* *Lemna minor*
2	0.4	4.0	Pasture	*Spirodela polyrhiza* *W. columbiana*
3	1.5	3.5	Wooded area	*L. minor* *W. populifera*
4	0.8	2.5	Pasture	*Pithophora* sp.
5	0.3	2.0	Minnow hatchery	*Pithophora* sp.
6	0.5	5.0	Pasture	None

[1] This study was financed by the General Research Fund of Southern Illinois University and by the Illinois Department of Conservation.

TABLE II. Dissolved oxygen, carbon dioxide and temperature of ponds supporting a surface growth of duckweeds or *Pithophora* compared to a pond without such growth

Pond No.	Date	Type Cover	Extent of Cover	Dissolved Oxygen ppm			Free Carbon Dioxide ppm			Temperature °F		
				Surface	One foot	Bottom	Surface	One foot	Bottom	Surface	One foot	Bottom
1	8/ 3/59	Duckweeds	Complete	0.0	0.0	0.0	60	75	90	76	75	74
	8/ 8/59		"	0.0	—	—	70	—	—	75	—	—
	8/ 9/59		"	—	0.0	0.0	—	80	101	—	74	73
	7/ 5/60	Duckweeds	Partial Increasing	3.0	—	0.0	18	—	—	79	—	83
	7/21/60		"	2.4	—	0.0	22	—	—	77	—	80
	7/30/60		"	3.6	—	0.0	45	—	—	78	—	50
	8/ 3/60		"	2.2	—	0.0	45	—	—	73	—	70
	8/11/60		"	1.5	—	0.0	70	—	—	71	—	70
	8/24/60		"	1.5	—	0.0	35	—	—	71	—	80
	9/28/60		"	1.0	—	0.0	33	—	—	70	—	80
	10/13/60		"	0.5	—	0.0	30	—	—	70	—	81
2	8/ 5/59	Duckweeds	Complete	0.0	0.2	0.2	60	38	38	79	76	72
			Partial	2.8	0.5	0.0	60	44	61	89	74	71
	8/24/59		Complete	0.0	0.4	0.2	70	41	38	78	74	71
			Partial	2.7	0.5	0.0	76	46	63	88	73	70
3	8/20/59	Duckweeds	Complete	0.6	0.8	0.2	60	43	46	78	75	73
			Partial	3.2	1.5	1.1	50	41	54	89	81	79
	8/26/59		Complete	0.3	0.7	0.1	64	44	49	77	75	72
			Partial	2.9	1.3	0.9	61	39	56	88	81	79
4	8/ 5/60	Pithophora	Complete	3.0	—	0.9	40	—	90	81	—	76
	8/17/60		"	0.6	—	0.0	55	—	65	80	—	74
	9/ 7/60		"	0.8	—	0.0	54	—	66	81	—	75
5	8/ 5/60	Pithophora	Complete	1.2	—	—	70	—	—	81	—	—
	8/17/60		"	2.0	—	—	63	—	—	82	—	—
	9/ 7/60		"	1.6	—	—	74	—	—	81	—	—
6	8/20/60	None	None	8.0[1]	11.2	1.3	8	18	53	91	90	83
	8/26/60		"	8.4	10.1	1.2	8	19	54	91	91	81

[1] Supersaturations probably due to presence of a unicellular, algal bloom.

the surface. The same was true of the 1959 observations on Pond 2, but not of the other ponds.

To observe further the effects of duckweeds upon the dissolved oxygen and free carbon dioxide content of water, observations were made under aquarium conditions. Two tanks (A and B) of the following description were utilized:

Steel tank with one end of glass
Contained 35 gallons of water
Surface area of water 770 square inches
Surface area of front glass 191 square inches
Illuminated 12 hours daily with 40 watt incandescent at 10 inches.

Both tanks were stocked with 200 guppies (*Labistes reticulatus*) and a quantity of duckweed (*Spirodela polyrhiza*) was added to tank A. After 2 months the duckweed had completely covered tank A. At this time chemical analysis at the end of 4 hours of illumination gave the following values:

Tank A dissolved oxygen 0.4 ppm; free carbon dioxide 37 ppm.
Tank B dissolved oxygen 5.4 ppm; free carbon dioxide 15 ppm.

From the foregoing observations it appears that a covering of duckweeds and to a lesser extent *Pithophora* constitutes a major influence in some aquatic environments.

RESISTANCE TO HIGH TEMPERATURES IN A MEDITERRANEAN SNAIL, *LITTORINA NERITOIDES*

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Much has been written in recent years on the adaptation of poikilothermic animals to the temperature of their surroundings (Bullock 1955, Prosser 1961). In many of the relevant investigations in this area the effect of temperature on metabolic processes was used as the criterion for such adaptations. Evidence also exists to the effect that adaptation to a higher temperature implies an upward shifting of the lethal temperature. I have, however, previously pointed out (Fraenkel 1960) that there is a relative lack of data on the tolerance of high temperatures by marine invertebrates, and that most existing data are useless owing to faulty methods and inadequate criteria. It was urged that the acquisition of comparable data necessitates adherence to these two principles:

1. Test temperatures should be constant instead of rising.
2. The criteria for heat injury and death should be rigorously defined for each species.

The most useful and sensitive criteria were the influence a particular treatment had on a typical behavior pattern of the animal, as in the examples previously under investigation: for *Limulus* the habit of digging into sand, for *Littorina* crawling up vertical surfaces and out of the water, and for naked *Pagurus* the reoccupancy of a snail shell. In *Limulus* and *Littorina* the lethal temperatures observed were relatively high. These were considered striking examples of adaptation in organisms which are habitually exposed to high temperatures, *Limulus* when stranded at low tide, and *Littorina* frequently out of the water and fully exposed to the sun and air.

The Mediterranean practically has no tides, and consequently no typical intertidal fauna. *Littorina neritoides* L., the only common *Littorina* in these waters, is not exposed to a regular tidal submergence rhythm, but is usually found out of the water in places exposed to waves and spray at irregular intervals. On rocky shores it is extremely common 1-2 meters above water level and it is known to survive exposure to air for many months.

The observations to be reported here were made in the area of Villefranche, Côte d' Azur, France during the summer of 1960. They originated from the assumption that *L. neritoides*, by virtue of its position high on sunlit rocks, must frequently be exposed to high temperatures. It was intended to obtain measurements of ambient temperatures, of body temperatures, and of the tolerance to high temperatures. Attempts at the first two did not yield the expected results. 1960 was a relatively cool summer. Rocks fully exposed to the noon and afternoon sun were not occupied by the snail. *Littorina* was commonly found only in places relatively protected from direct and prolonged exposure to sun, as on northern and north-eastern faces, in crevices, near the water level, or in higher positions frequently wetted by waves or spray. This made it improbable that they would ever be exposed to extremely high temperatures. Body temperature measurements attempted with a thermistor thermometer did not succeed owing to the small size of *L. neritoides*, the largest specimens measuring 5 mm across and 7 mm from base to apex.

The resistance of *L. neritoides* to high temperatures was determined in the laboratory, using exactly the methods described previously (Fraenkel 1960). The snails were immediately plunged into sea water kept constantly at the desired temperature. Batches of 10 were withdrawn after exposures of suitable duration, and transferred to small battery jars containing about 5 cm of sea water and left standing at room temperature. Recovery was judged complete if the snails were able to pass through the successive motions of stretching out of the shell, becoming fixed to the bottom of the vessel, crawling to the glass wall, and then vertically up and out of the water. With incomplete recovery they came out of the shell without becoming affixed, or became affixed without further locomotion, or did not come out of the water. Snails showing signs of incomplete recovery usually died within a few days. For the purpose of the present investigation it was found sufficient to record the number which had crawled out of the water and the time when this was observed.

The data obtained are assembled in 2 tables. Table I merely records the number of animals that completely recovered from exposure for different durations to different temperatures. Table II gives details of the recovery periods of snails exposed to 48°C in air for various durations. The results show unequivocally that a water temperature of 46°C was well tolerated for periods of 2 hours, that about 50% died after exposure to 47°C for 90 minutes, and that even 48°C may be sustained for 30 to 45 minutes.

Table I. The effect of high temperatures on the survival of *Littorina neritoides*. Each figure represents the number of snails, out of 10 that recovered within a period of 3 days. Criterion for recovery: crawling out of the water spontaneously

Temperature °C	Date 1960	Location	Minutes of Exposure								
			30	45	60	75	90	120	180	240	360
Exposed to sea water											
46°	6/30	A	7	7	7	6	5	—			
46°	7/21	E	—	—	10	—	10	8			
46.4°	6/21	A	9	10	7	8	6	—			
46.5°	7/4	B	—	6	8	—	5	—			
46.5°	7/4	C	—	7	10	—	3	—			
46.5°	7/4	E	—	9	8	—	10	—			
47°	7/21	E	—	8	10	—	9	—			
47.3°	6/28	A	10	5	4	3	4	—			
48°	6/12	A	1	0	0	0	0	—			
48°	6/30	A	2	0	0	—	—	—			
48°	7/21	E	8	4	2	—	0	—			
49°	7/21	E	1	0	0	—	—	—			
Exposed to air											
45°	6/23	A	10	8	7	9	10	—	—	—	—
48°	6/28	A	9	10	10	10	7	—	—	—	—
48°	7/26	E	—	—	10	—	—	9	8	6	0
48°	7/26	D	—	—	8	—	—	4	7	2	0
50°	6/30	A	8	3	3	3	2	—	—	—	—

Locations from which snails were collected: A, B, C and D: Bay of Villefranche. A: Rocks up to 1 m above water level. B: Somewhat lower, continuously wetted by waves. C: Between 1 and 2 m above water level. D: From a rock pool, apparently permanently submerged. E: Rocks near Hyère. Up to 1 m above water level.

These data are not immediately applicable to the ecology of *L. neritoides* which spends most of its life out of the water and is never naturally exposed to such high water temperatures. In a further series of tests the snails were exposed to high air temperatures in a drying oven. The tests were arranged so that the opening of the oven and

TABLE II. Course of recovery of *Littorina neritoides* from an exposure to a temperature of 48°C in air for 1 to 6 hours. Experiment of July 26, 1960 (Table I)

Hours of exposure	Number of Snails Recovering After Days					Condition of Snails not Recovered on 6th Day	
	½	1	2	3	4	alive	dead
1.....	1	5	1	—	1	2	—
2.....	—	—	3	—	1	2	4
3.....	—	1	5	1	—	1	2
5.....	—	1	—	—	1	—	8
6.....						—	10

withdrawing of samples could be performed with the utmost speed, involving only brief drops in temperature. In air, the snails survived temperatures 2° higher than in water; 48°C was tolerated for 3 hours, and some individuals survived even 50° for 90 minutes. This difference in resistance could be due to several factors, the longer time required to attain the temperature of the surroundings in air, the drop in temperature when the oven is opened, and the cooling effect from evaporation of water. The small size of the snails, the efficient protection provided when the shell is closed by the operculum, and the slight drop in temperature upon opening the oven make no one of these factors seem significant. However, the combination of all three may well have lowered the body temperature to the extent indicated by their higher resistance in air. Altogether, it is not probable that the mere fact of being in air would be of survival value at a given body temperature, the less so since the opercula are firmly closed at the temperatures in question, both in air and water. It is, therefore, assumed that the heat resistance depends solely on the actual body temperature, irrespective of whether the snail is in water or air.

Table II has been inserted to show that recovery from an exposure to high temperature is slow and, in this test, was delayed up to 4 days. As one would expect, recovery is faster the milder the treatment, but even with the shortest exposure time of one hour in this experiment, with 8 out of 10 snails recovering, only one had crawled out of the water within 12 hours.

The observations recorded in Table I also throw an interesting sidelight on possible differences in heat resistance encountered with populations from different localities and with different ecological characteristics. Most of the tests used snails from rocks between the town and harbor of Villefranche, with a distinction made between those sitting near the water's edge and continuously wetted by the waves (B), those up to about 1 meter above (A), and those still higher, between one and 2 meters above the water level (C). At a 4th locality on the opposite shore of the bay snails (D) were discovered submerged in a rock pool and showing no sign of ever leaving the water. These snails, however, when observed in the laboratory, crawled out of the water as readily as those collected out of the water. Populations of *L. neritoides* which remained permanently submerged were also observed by Lysaght (1941) at the Plymouth Breakwater. A 5th supply of snails up to 1 meter above the water level was collected from rocks near Hyère, about 150 km further west (E).

The suggestion of differences in the heat resistance of different populations arose too late to be submitted to a rigorous examination. The data so far obtained (Table I) suggest strongly a higher degree of resistance in the population from Hyère (E) and, in the one existing test, a lower resistance in those permanently submerged (D).

A comparison of the data reported here for *L. neritoides* during the summer in the Mediterranean with corresponding data for a related species, *L. littorea* in August at Woods Hole (Fraenkel 1960) reveals the former to tolerate a temperature 6° higher. 40°C to 41°C is tolerated by *L. littorea* for between 1 and 2 hours, against 46°C-47°C by *L. neritoides*. These figures agree poorly with those given for lethal temperatures of the same 2 species from the shores of Cardigan Bay, Wales (Evans 1948). No direct comparison of absolute figures is possible, as pointed out previously (Fraenkel 1960), since the snails from British waters were submitted to a slowly rising temperature and the criterion for recovery was merely a local reaction to prodding by a needle. Considering these differences in method, the figures for *L. littorea* in the 2 investigations agreed fairly well (Evans 46°C, against Fraenkel, using Evans' method: 45°C). However, Evans, using sliding temperatures found the same figure (46°C), for *Littorina neritoides* and *littorea*, and approximately the same tolerance in the 2 species on prolonged exposure to 40°C. In my investigation the tolerance differed by as much as 6°. To what extent the differences in resistance of *L. neritoides* from greatly different ecological localities may be real, or are due to the different methods employed, cannot be decided at this point.

A tolerance of such high temperatures as recorded here for *L. neritoides* in the Mediterranean is most astonishing and has rarely, if at all, been recorded under comparable conditions. Omitting typically terrestrial forms such as insects or reptiles, where similar temperatures have been recorded in a few instances (Prosser 1950) the highest relevant data concern *Limulus* (44°C for 1 hour, Fraenkel 1960).

Restricting ourselves to data obtained by comparable methods, marine invertebrates in temperate zones usually do not resist temperatures above 35°C for any length of time. No well documented data appear to exist for tropical waters. The relatively high temperature tolerance of the various species of *Littorina* is obviously connected with the fact that these organisms pass most of their lives, though in a passive state, out of the water. By comparison, a species of *Trochus* occurring in the Mediterranean in close proximity to *L. neritoides*, tolerated a temperature of only 40°C for 1 hour when tested under identical conditions. This *Trochus* also crawls out of the water, but rarely more than 30 cm above the water level, and either in places not reached by the sun, or where it is continuously wetted by the waves and spray. Considering the group of *Littorina* in general, and *L. neritoides* in particular, we are dealing here with an example of an extraordinary temperature adaptation in organisms which are habitually exposed to high temperatures. There is no particular reason why a marine organism which is permanently submerged should be expected to resist very high water temperatures since the temperature of sea water rarely exceeds 30°C anywhere in the world.

SUMMARY

The lethal high temperatures were determined for a Mediterranean littoral snail, *Littorina neritoides* L. which spends most of its life on rocks out of the water. This snail resists 46 to 47°C for 1-2 hours when submerged, and temperatures about 2° higher when in air. A tolerance to such high temperatures has apparently never been recorded before in a marine invertebrate under comparable conditions. This is considered as a case of an ex-

traordinary temperature adaptation in an organism which is habitually exposed to high temperatures.

ACKNOWLEDGMENT

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THE DISAPPEARANCE OF *CYATHURA POLITA* FROM THE ASHEPOO RIVER, SOUTH CAROLINA, AFTER HURRICANE "GRACIE" IN 1959[1]

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The Ashepoo River in the state of South Carolina is a dark water river (Figure 1) which flows into the Atlantic Ocean about 30 miles south of Charleston. It is unusual in that it is quite short, being around 35 miles in length. The river is free of industrial wastes and, except for the extreme upper reaches of its headwaters, it is under tidal influence. Although the lower two-thirds of the river meanders, there is a strong current that sweeps the clay-marl sides of the river free of most debris. Dredging, however, showed an accumulation of soft, organic material in the bottom of the central channel.

FIG. 1. Upper reaches of Ashepoo River, South Carolina, April 4, 1959.

Over a period of 3 years (July 13, 1956; April 4 and 23, 1959) collections were made at 3 stations along the river, and the estuarine isopod, *Cyathura polita* (Stimpson) (Miller and Burbanck 1961) was found in all of them. The largest population of cyathurans was at a shell ramp for launching boats which was adjacent to the bridge where U. S. Route 17 crosses the Ashepoo River (Burbanck 1959). Cyathurans were also located at another shell ramp about 10 miles upstream from Route 17 (Figure 2), and about a mile downstream from the highway in sand caught by the rock ballast under a railroad bridge (Figure 3).

It was a surprise on October 31 and November 1, 1959, after diligent searches using both spade and dredge, to find no *C. polita* at any of the 3 locations. Gammarids and nereid worms usually found in the same association were also lacking. Upon traversing some 3 miles of the Ashepoo River by boat, it was apparent that Hurricane "Gracie," which struck the Charleston area Sept. 29, 1959, had wreaked great havoc. Along both the Ashepoo River and the Edisto River several miles to the north, large pine trees were snapped off and many red cedars (*Juniperus virginiana*) uprooted.

According to newspaper accounts in Charleston, the hurricane was attended by the heaviest rain in 100 years, and also at that time there was a very high tide. Upon inquiry, Mr. Joseph Smith, who runs a fishing camp by Route 17, said that after the hurricane there was a tre-

FIG. 2. Low tide at Price Landing, Horseshoe Creek (northern fork of Ashepoo River), April 4, 1959. Shell ramp at extreme left center.

[1] Research supported by National Science Foundation Grant G-7138 and the McCandless Fund of Emory University.

FIG. 3. View of rock ballast at low tide taken from under R. R. bridge, Ashepoo River, South Carolina, April 4, 1959.

mendous fish kill. So many fish died, in fact, that they clogged the river at the bridge, and it was necessary for him to clear away the jam as the fish began to decompose.

Mr. Smith observed the following fresh and brackish water fish among those killed: bream, bass, carp, catfish, jackfish, mullet, and eel. He specifically mentioned that he did not see dead mud fish or gar. He noted that when the fish were dying, all species came to the surface and seemed to be gasping for air.

In 1956, Lunz reported large oyster kills in the Chesapeake Bay area after hurricanes "Connie" and "Diane" in 1955. These kills were also correlated with heavy rain-falls (16 inches in 5 weeks). Since it is difficult to see how rainwater *per se* would have a harmful effect on cyathurans and freshwater fish, other possibilities need to be sought. Dr. Harold Humm of Duke University (private communication) has suggested that the stirring up of organic material in the river might have released enough hydrogen sulfide to kill both fish and isopods. Also, with regard to the isopods, large amounts of sand washed from roads into the river might have covered and smothered them, and the tannins from many leaves carried into the river may also have had a toxic effect.

Ten months after Hurricane Gracie (July 22-23, 1960), another trip was made to the Ashepoo River and the 3 stations previously studied as well as a 4th one about 10 miles downstream from Route 17 were thoroughly investigated. No cyathurans were found, but Mr. Smith reported that catfish had been caught in the river.

Although it was a blow to lose the Ashepoo River population of cyathurans since it was readily accessible and a stable population, it will be of great interest to keep this river under observation and try to ascertain if and when recolonization takes place. Of course, it is possible that all cyathurans were not killed and that they will reestablish themselves from the remnant. Another source of animals for recolonization might possibly be known populations (Burbanck 1959) in estuaries to the north or south of the Ashepoo River.

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REVIEWS

Trees, Woods and Man[1]

"Trees, Woods and Man" is a volume in the New Naturalist Series that has been appearing in England for some years. It is divided into three main parts, the first of which is entitled "The Natural Setting," the second "Man's Influence on the Forest," and the third "Studies of Particular Trees." Part I, consisting of five chapters, deals with the major features of the structure and development of trees, the relation of individual trees to the assemblages of others among which they grow, and with the principal elements of the physical and biological environments. Part II is, in this reviewer's opinion, the most significant part of the book. It contains the author's attempt to reconstruct the history of British forests from prehistoric times to the present. Part III contains 14 chapters and is organized by genera of trees. These chapters on the common trees in British forests summarize existing knowledge of the distribution, silvics, properties, and uses of the various species.

The book is plentifully illustrated with 24 plates in color, and an equal number in black and white. There are two text figures, one of which is a map showing the distribution of woodland in Britain in 1954. At the close of the volume there are some short notes on the uses of terms, a bibliography of the principal works consulted, and a rather comprehensive index.

In America we are fortunate in having a kind of "datum plane" from which to begin the reconstruction of the history of our vegetation. This is the time of our earliest settlements in any given part of the North American continent. Students of vegetation in most of Western Europe and Britain, on the other hand, have had no such well-defined datum plane, for the intensive use of the land by man goes far back into prehistoric times. The author of this book fully realizes this, but conceives that an understanding of the present condition of British woodlands must be based solidly upon as complete a knowledge as can be gained of the way the lands in Britain have been used by man. He utilizes a variety of evidence in outlining this history: from the fields of archaeology, ethnology, studies of fossil pollens and other plant parts preserved in various kinds of deposits; and of course the written records of the Roman occupation of Britain. The Domesday Book (ca. 1086) was a major landmark because it presented what amounted to a forest inventory for the time.

The economy of British and most Western European forests is far different from that of American woodlands, for it is based upon a scarcity of wood rather than upon the relative abundance that we have always had on this side of the Atlantic. In Britain this scarcity became particularly serious at the end of the First World War, when the nation had used up nearly all of its existing domestic timber resources. At that time a Forestry Commission was instituted for the express purpose of reestablishing forests in Britain as rapidly and as widely as possible. The Commission was given broad powers for the acquisition of land, and large financial resources with which to forward its work. Mr. Edlin's book gives a résumé of the accomplishments of the Forestry Commission up to 1954, and it is indeed impressive.

It was decided by the people of Britain that it was in their national interest to have a certain percentage of their land in productive forest, and they expressed their willingness to invest their public money in it. The wood that will be grown on the afforested areas probably will be expensive wood, not merely because of the cost of the land, the planting, the protection of the growing forests and the management of these forests throughout their long period of growth to commercial maturity, but also because of the cost of holding the initial investment for so long a time. But the values to be realized are not all those that can be measured in simple financial terms, and these intangibles must be given full consideration. They include insurance that the nation will have some stocks of wood in time of war or dire economic stress, and there is a large element of what the British like to call "amenity" values. This kind of investment needs no apology or defense. It can stand on its own merits, and there was ample precedent for it among the nations of Western Europe.

The author believes that the most important single factor determining the present distribution and much of the present condition of British forests was the enclosure movement in the development of land-use patterns. This movement was accentuated in the 17th and 18th centuries, though it began on the great feudal estates much earlier. It appears to have begun with the enclosure of forested "parks" on some of the better soils in the immediate neighborhoods of the large manor houses. The purpose of these parks was not for the management of their forests, but rather for the preservation of hunting privileges. Only secondarily and much later did the use of the forested enclosures for timber assume any significance. The establishment of the great plantations in Britain was greatly influenced by motivations of patriotism and the purely aesthetic interests of the time, and did not occur on a large scale until the 18th and early 19th centuries. As the author says, the great planting landowners could not have carried on their work on such a large scale without "a sound economic background." This economic background had arisen out of the system of money rents that came from tenants of the enclosed lands. Thus the landlords were acquiring large capital resources, and among other things they put considerable sums into the planting of trees.

It is of interest to note, however, that "toward the latter half of the 19th century this great wave of afforestation, carried out by numerous landowners in nearly every county of Britain, began to slacken off." The author gives various reasons for this, but he gives as probably the largest single factor the "increasing range of opportunities for other forms of capital investment brought about by the Industrial Revolution at home and the growth of commerce abroad." In other words, when there was a better outlet for their capital, the landowners lost interest in the planting of forest trees. All this suggests that capital investment in British forests in the past has been made with a bundle of motives, but that the motive of economic gain has never been a very significant one.

In spite of this history, Mr. Edlin seems to have no hesitation in describing the forestry operations on British estates or on the Forestry Commission land as sound business ventures, repeatedly neglecting to analyze their real

[1] Edlin, H. L. 1956. Trees, woods, and man. Collins, London (The New Naturalist, no. 32). xv + 272 pp., 2 figs., 24 color and 24 black & white plates. 30s., $4.50.

costs over time, and failing to take account of the risks and uncertainties that are involved. It is only fair to say that markets are more stable in the Old World than they are in America, and that risks are perhaps more readily predictable. But in these days of rapid advance in wood technology, and of the extraordinary variety and efficiency of substitutes for wood, and of new sources of power, who can make reliable predictions beyond a few years as to how much wood we will use or how we will use it?

Mr. Edlin's book is marred on many of its pages by the free use of pejorative terms when these terms appear to be thoroughly unjustified. There are many instances of this that could be cited, but one will suffice. On pages 97 and 98 the author describes the use of the manorial woods and commons in medieval England. He speaks of the "constant abuse" by the peasants of the right to gather firewood, and describes this and other practices as "haphazard pillage." Then, on the next page (99), there is the statement that "A factor that worked against the planned preservation of timber was the lack of any real element of cash profit in its sale." One wonders whether, under the circumstances, such practices ought to be called "abuse" or "pillage." Were they not merely the normal use of the woods within the terms of the existing or foreseeable social and economic structure? To call them by these terms is merely a gratuitous projection backward of our own values.

Having written these few critical remarks, this reviewer hastens to recommend Mr. Edlin's book highly. It is informative and eminently readable. It contains most of the essential facts about forests and forestry in Britain, and one is at liberty to make his own interpretation of them. But the book is much more than a recital of facts about British forests. Many who find their major interests in land and resource management, and in the origin and development of the institutions concerned with these things, will read the book with pleasure and profit. Anyone who plans to go to Britain for any purpose that is concerned with the landscape or its history should consider it essential background reading.

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Forest Fire: Control and Use[1]

Forest fires evoke strong emotions. These include fascinated excitement at the sight, instinctive fear, and abhorrence of the aftereffects.

Much of the literature dealing with forest fires reflects some antipathy of the authors toward fire. Dr. Davis' treatment, however, is carefully designed to create an objective viewpoint. This objective treatment starts with the title and is woven into the text with a skill that reflects his long experience as a teacher. He starts by pointing out that, next to soil and climate, fire has been the most important determinant of vegetative cover on wild lands. After he has discussed the engineering aspects of fire control, he ends the book with a discussion of intentional use of forest fires. Despite his disclaimer of neither advocating nor condemning this use, the reader may gain the impression that he regards prescribed burning as a desirable forest-management operation under the right conditions.

This textbook is intended primarily for undergraduate forestry students. As such, it fills an important gap in forestry literature, since it is the first hard-cover text dealing solely with forest fires. But it also should serve as a useful reference and refresher for practicing foresters, since the text and bibliography together include reference to most of the literature on the subject, much of which has been written in the last 10 to 20 years. As would be expected, over three-quarters of the book deals mainly with fire behavior and fire control. This part of the book may be of less interest to ecologists than the smaller part that considers the effects of fire and its beneficial uses.

The text is separated into three parts. In the first section, the major discussion of fire effects ends on page 60 and of fire behavior on page 228. The subject of the second section is the control of forest fires—occupying another 252 pages. The last and shortest section—Fire in Forest-Land Management—deals with objectives and history of fire control and with use of fire in forest management. The main consideration of effects of fire is in two chapters in the first section and the description of use of fire is in two chapters in the last section. However, chapters on forest fuels and hazard reduction also discuss the problems of fire effects and prescribed burning.

The first chapter—Fire in the Forests—introduces and defines the subject, describes 10 of the large fires in the past century and a half, and ends with a brief survey of the effects of fire in some of the major forest types in the United States and Canada. This survey is based on first-hand observation as well as thorough review of the literature and is one of the best summaries of its kind that I have seen. It should convince even the most casual reader that fire was an important force in determining the forest types found by our forefathers, and that it may be a useful tool in managing some of the extensive subclimax coniferous types that we value highly today. But the survey also demonstrates the dangers of generalizing about forest fires. In some areas, fire maintained subclimax types; in others, it helped perpetuate climax types; and in yet others, it helped to introduce temporary types after logging and land clearing.

The next chapter—Fire Effects—takes up the results of fire on the components of the forest. It starts with individual trees, briefly mentions other vegetation and microclimate, and discusses effects on soil at some length. Although there are warnings that there are serious gaps in knowledge about fire effects, these hiatuses are hard to identify. Perhaps it is a useful teaching device to state mooted points as firmly as those that are generally accepted, but I feel that it detracts from the reference value of this chapter. To soften this hypercritical comment, I should add that it would be well-nigh impossible to summarize and evaluate the available literature in a span of 30 pages.

Viewing vegetation as fuel may seem a novel approach to ecologists. Yet this is done in chapter 6—Forest Fuels. Foresters generally use cover types to describe fuels, although they do not find these classifications entirely

[1] Davis, Kenneth P. 1959. Forest fire: control and use. McGraw-Hill Book Company, Inc., New York, Toronto, London. xiii + 584 pp., 78 figs., 30 tables, $12.00.

satisfactory. To improve these the author suggests the engineering approach of calibrating fuels in terms of rate of heat-energy release. However, the amount of fuel (vegetation) on any area depends on the productive capacity of the site and the activity of micro-organisms in reducing dead material, and the type of fuel is determined by the plant associations found on the area. It is hard to see how the more refined descriptions that are needed in fire control can omit these basic facts.

Hazard reduction has the special meaning of reducing or eliminating flammable material. This may seem mostly a mechanical cleanup job, but there are opportunities in many regions to substitute less flammable vegetation for existing hazardous cover types. Indeed this may be the only practicable way to prevent major fire disasters. Chapter 9 provides a general description of the problem.

The major uses of fire in forests in the United States are generally covered in chapter 18. This is intentionally painted with a broad brush. It is surprising to find more space devoted to uses in range and wildlife management than to other uses, but this is offset in part by the more detailed considerations of hazard reduction and silvicultural uses in the case examples in chapter 19. These case examples mention the need to consider the ecology of the area in planning prescribed burning, but offer little specific information about these considerations. Going back to the chapter on fire effects, we find that many, but not all, of the important considerations are mentioned. The excellent bibliography can be used to obtain further information.

I feel that this book is an outstanding source of general information and perspective for those interested in the ecological aspects of forest fires. However, it was not designed to be a reference work for specialists. The illustrations are excellent and editorial lapses are minor.

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Russian Forest Influences[1]

This paper-bound book is a translation from the Russian of Prof. S. V. Zonn's "Influence of the forest on soils," published in 1954 by the Academy of Sciences of the USSR as part of their "Scientific-Popular Series for Aiding the Rural Economy" at 2 rubles, 65 kopeks. The book is not a universal treatment of its subject. Zonn limits himself to his own area of experience—which is vast enough; but even within the USSR, Mediterranean, Pontic, far eastern, and Central Asiatic relict, desert, and mountain forests of various kinds are not mentioned. Some mountain forests of the Caucasus and Bulgaria are compared with the latitudinally zoned forest of the lowland USSR.

The German edition is really a new one with some additional material (on p. 158, e.g.), and the translation upgrades the book not only in cost but also in quality of printing and binding. The contents fully deserve this increased attention.

Essentially, Zonn reviews and briefs the contents of a number of extensive Russian monographs on relationships between particular forests and their soils. These include oak forests in the forest-steppe, *Pinus silvestris* forests on sandy soils, nutrient cycles in taiga spruce forests, the influence of shelterbelts on solonetz and chernozems, etc. He does more by putting the data into a logical arrangement, with adequate additions from the large backlog of Russian work on forest-soil relationships to round out his theme.

Zonn makes the point in his foreword that a forest is more than a haphazard agglomeration of trees. It is an ecologically determined system. It turns out however, that Morosov, who occupies a position in Russian silviculture analogous to Dokuchaiev in pedology, originally defined the forest as an "organism" (p. 6 German edition, p. 11 Russian). In the German edition this comes out as a "system"—a happy choice. Unfortunately a little farther on Morozov's characterization of the forest as a complicated natural phenomenon comes out as a "formation." The plant geographical use of "formation" is not intended and will confuse.

After spending a very few pages outlining the forest cover of the USSR, with a zonal map of the European part, Zonn considers the forest as a kind of biogeocenose or ecosystem. Next in 8 pages the main forest trees of the USSR are described, particularly in their soil relationships. Then the typology and soil relations of various kinds of spruce forests, of pine forests, of oak forests, and of larch forests are discussed. Analyses of soil profiles by horizons, including the organic layers, tables correlating forest types and soil types, and diagrams and photographs illustrating such correlations enrich this chapter.

A major section of 36 pages considers the role of litter and the humus horizons in the changes occurring in forest soils. Variations in amounts of litter fall with species, forest type, age of stand, site index, and soil type are tabulated. Destruction of the humus layers by invertebrates is achieved by astonishingly high numbers of animals, whose excreta in one case are said to equal 0.6 to 1.0 $g/m^2/24$ hours. The water and CO_2 economy of humus layers conclude this section.

Tree roots in forest soils reach amounts of almost 80 tons/ha, but as interesting are the variations in amount in different forests. The contributions to the soil by the ash of roots and as water soluble substances are detailed qualitatively and quantitatively.

A most interesting chapter of only 8 pages follows, giving quantitative data on the circulation of organic and mineral substances between the forest vegetation and the soil. The ash amount added to the soil under an oak forest may be some 10 times that under a spruce forest. This is truly quantitative plant ecology. Unfortunately, data on tropical nutrient cycles are not mentioned.

The final section considers the influence of the forest vegetation on some properties of the soil—on the water balance, on the composition of the soil air, and on the humus content. Here numerous data accumulated in the course of shelterbelt establishment are used. These data represent experimental plant ecology on a grand scale. The point is made again here that "the forest" has no uniform influence on the soil. Its influences depend not

[1] Sonn, S. W. 1960. Der Einfluss des Waldes auf die Böden. (Translated from Russian, 1954, by Peter Kundler) Gustave Fischer Verlag, Jena. xii + 166 pp., 28 figs. 13.40 DM ($3.20).

only on the kinds of trees that can grow in the area but also on the ecological conditions of the site.

This is a small book on a large subject. It does make readily accessible many important data, and it puts them into a logical exposition. The few cases of quoted but missing references will probably bother no one since *all* the references have been essentially unused. Language students will welcome the possibility of using parallel texts in Russian and German. Ecologists will welcome this book for its ecological viewpoint making available quantitative data on particular forests and forest soils. Foresters will welcome it for its use of silvicultural ideas and data in an ecological context. The fact that the book has a universally applicable title but is actually quite narrowly geographically limited merely reflects the undeveloped state of plant ecology, silviculture, and pedology.

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The Botany and Plant Ecology of Arnhem Land[1]

Arnhem Land is part of the Australian Northern Territory, lying immediately to the east of Darwin. It forms an aboriginal reserve, and consequently visits by scientists are rather rare. In 1948 an expedition organized jointly by the National Geographical Society of America, the Smithsonian Institution and the Australian Government visited the area and made extensive collections in six localities near the coast. The present volume does not indicate how long was spent in the region or at what season of the year the expedition took place.

This volume describes the plant collections resulting from the expedition, and includes also extensive comments on climate, geology, soils, vegetation, and ethnobotany. The main collections were of vascular plants, but there were also a considerable number of freshwater and marine algae collected and smaller numbers of fungi, lichens and bryophytes. Each group of lower plants is described by a specialist, while the spermatophytes are described by R. L. Specht, the senior Editor, who was also the botanist accompanying the expedition. These systematic chapters form about two-thirds of the volume. The collections included a substantial number of new species and varieties—particularly among the freshwater algae and the angiosperms—and the volume includes diagnoses of these new taxa. The value of the book is increased by notes on collections made by others in the interior of the region, which the expedition did not visit.

The section which will be of greatest interest to readers of Ecology is obviously that dealing with the habitat and vegetation types found. The climate of the area is tropical and strongly monsoonal, with heavy falls of rain during a limited period of the summer and a very dry winter. The major types of vegetation occurring are consequently open woodland (dominated by *Eucalyptus tetrodonta*) and savannah woodland of various types, though favourably situated areas may have small patches of monsoon woodland approaching rain forest in structure; freshwater marshes, and mangrove and other strand communities are also included. These vegetation types are described by Specht in terms of associations designated by the dominant species, and in many cases grouped in edaphic complexes where varied soil development within the same climatic conditions leads to vegetational differences. The accounts of these communities are almost entirely of a descriptive character, and are supplemented by species lists which carry no indication of how important the various species may be. Such lists may be of autecological value, indicating the associates with which each species may be found; synecologically, they do no more than whet the appetite. In the case of the *Eucalyptus tetrodonta* community only is more extensive tabulated information given, indicating the commonness of each species in six different stands. Incidentally, this table shows as occurring (or even "common") in certain stands of the community a number of species which are not listed for that community in the main table. It is clear that one cannot expect too much ecological detail from an expedition whose prime purpose was taxonomic collections; but one wishes that rough quantitative data had been collected and published for a number of stands of each of the communities, and not only for the *E. tetrodonta* woodland.

Attention is drawn to the similarity of many of the vegetation types to those in the Darwin-Katherine Area to the west, described by Christian & Stewart. The affinities with vegetation types in North Queensland, 500 miles to the east, are hardly mentioned.

Good photographs are given of most of the communities described, and there are detailed maps of some of the localities from which the collections were made. A tentative vegetation map of the whole of Arnhem Land is also included, for which the detailed records from coastal collecting stations were supplemented by the results of aerial survey.

The chapter on ecology is followed by one on the plant geography of the area. The angiosperms of Arnhem Land include a considerable number of endemic species, most of the others being common to various regions of northern Australia and New Guinea. There is a strong Indo-Malayan element, and also a large pantropical group of species. Among genera of Australian origin, it would seem that extensive speciation has occurred in northern Australia. This chapter on plant geography also deals at some length with the geological history of the area, in an attempt to illuminate the origins of its flora.

The volume is completed by an index, but on examination this proves to be disappointing. It consists exclusively of the scientific names of plants, and the references (except for the freshwater algae) seem to be only to the lists and tabulated material. Ecologists are likely to be much more interested in finding where a plant is referred to in the descriptive text; in this they will be disappointed.

All in all, though, the book is a very creditable piece of scientific publication. It is well printed on good quality paper, with careful documentation and abundant illustrations. No misprints were noted. Clearly not very many individual botanists will wish to own their own copies; but it will be essential for any botanical library with Australian interests.

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[1] Specht, R. L. and C. P. Mountford, editors. 1958. Records of the American-Australian Scientific Expedition to Arnhem Land. 3. Botany and plant ecology. (Symposium) Melbourne University Press, Carlton, N.3, Victoria; Cambridge University Press, London and New York. xvi + 522 pp., 18 figs., 22 tables, 17 plates. $19.50.

The Biology of Weeds[1]

A large group of weed researchers gathered at Oxford University for three days in April, 1959, to participate in a symposium on numerous aspects of the biology of weeds. A year later this symposium was published under the editorship of John L. Harper for the British Ecological Society.

The 25 chapters of this symposium illustrate amply and refreshingly that there is much worth knowing about weeds beyond herbicidal dosages, volumes, carriers, formulations, nozzle designs, and the like. Weeds are fit subjects for studies in not only agronomy and horticulture, but also in taxonomy, genetics, ecology, physiology, evolution, archaeology, and palynology. The topics are arranged under 6 headings: Taxonomy and Evolution; Dormancy and Dispersal; Population studies; Interference and Competition; Special problems; and Autecological studies. Seventeen of the articles are authored by Britains, the remainder by biologists from Germany, Holland, Ceylon, New Zealand and Tanganyika:

A weed is a higher plant which is a nuisance, a plant which interferes with man's activities. Other useful definitions are offered by different authors of this symposium, for example, a plant is a "means by which one seed produces many seeds."

Most of the potential controversy over the difference between competition and inhibition is dissipated by the proposal of an inclusive definition of competition. Bleasdale used it as a process which exists when the growth of any plant is modified in association with other plants as compared with its growth or form when growing alone. The components of competition react in a total fashion which can be integrated only by the plant. Competition for the familiar light, moisture, and nutrients is sometimes associated with toxic substances or "kolines" formed by one species and toxic to another. Vanillic and p-hydrobenzoic acids and other phenolic compounds, are among these. Studies of these substances have been under way in America recently and are continuing.

Weeds have harnessed many agents of dispersal, man most successfully of all. While weeds are camp followers of man, their presence in natural seral communities has been shown by fossil-pollen evidence to predate agriculture. Neolithic man, 5,000 years ago, started the trend from forest to heathland in the British Isles when he began clearing for wheat. Sheep and rabbits were not the instigators, as explained by Godwin.

Many of the weeds discussed are strangers to United States' agriculturists, a fact that is not especially important since the authors used the weeds to illustrate basic findings.

One's concept of host specificity requires adjustment on learning that certain mistletoes of Ceylon, of which numerous species exist, are shown by Weeraratna to self-parasitize their own species, as well as others. Yet a degree of immunity from mistletoe is apparent in pear trees which have suffered mild attacks of mistletoe.

As the numerous, world-wide research problems on weeds are unfolded, one is impressed that weeds differ but little from continent to continent. Gorse, lupine, rose, willow, as described by Little's paper are similar ecologically in New Zealand and in various parts of United States.

A series of wide-spread plantings of three species of plantain by Sagar and Harper led to the conclusion that all adapted sites on the "Tight Little Isle" are already occupied by these species. Harper points out that elsewhere around the earth man is removing barriers to migration of diverse weeds providing opportunities for hybridization, allopolyploidy, and introgression.

Several of the topics are expounded in highly erudite language. The current graduate student in weed control, or his professor, should enjoy this recent book in his field immensely with the aid of good scientific and English dictionaries. Otherwise, such gems of palynology as the "descent of modern crops from ruderals of ancient middens" may escape him. Properly equipped, the student is certain to be intrigued and stimualted by many new ideas found in this work. To mention a few: the family-size to pasture-trend chain worked out by Chadwick, the water hyacinth calamity in Africa as observed by Gay, the technique displayed by Martin and Rademacher in studying stimulatory and inhibitory root exudates, the poisonous gas warfare between plants cited by Grummer and Beyer, the futility of weed control legislation, and seed dormancy classes proposed by Harper.

The life history study of Cirsium and Tussilago by Bakker provides an excellent model for similar research as does each of the papers of the last section on autecology of weeds.

The book is completely free of typographic errors because of the attention to detail by Buckles and Lauchbury. It is regrettable that they did not provide the book with an index.

Certain statements can be questioned, for example, the un-British exaggeration by Prichard that St. Johnswort occurs throughout the United States. In his thorough report on the adaptability of *Allium vineale,* Lazenby comments that deep bulbs are larger than shallow ones because more food is required for growth of the shoots. Teleology? Bunting's choice of the term "closed community" in preference to "natural vegetation" had best be understood as the "relatively closed community" inasmuch as it is also difficult to find.

Every student and worker in the field of plant science and especially ecologists will want to dip into this book.

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[1] Harper, John L., editor. 1960. The biology of weeds; a symposium of the British Ecological Society. British Ecological Society Symposium No. 1, Blackwell Scientific Publications, Oxford, and Charles C. Thomas, Springfield. xv + 256 pp., figs. & tables. $9.75.

The Mycorrhizae[1]

Every mycologist or plant pathologist, whether or not he thinks of the fungi in the mycorrhizal association as parasitic; every physiologist, whether he thinks of the absorptive phenomena resulting from the mycorrhizal association as abnormal physiology; every ecologist who must work with plants bearing mycorrhizae, will find this a most useful summary of our current knowledge of the mycorrhizal phenomenon.

The book is divided into three parts. The first, entitled "General Considerations," treats of the different types of associations between the roots of vascular plants and the mycelia of fungi. The second part considers the "ectotrophic mycorrhizas" in detail, while the third takes up the more heterogeneous "endotrophic mycorhizas."

The ectotrophic mycorrhizae are described in detail as to morphology and anatomy, illustrated by photomicrographs and drawings of the structures involved. Mycorrhizae of beech and pine are described separately and the development of their structure from the seedling stage onward is described carefully. The fungi forming mycorrhizae are considered next. Different species definitely associated with such root systems are indicated for certain trees. The activities of these fungi in pure culture are described and some of the problems associated with isolation and study of the organism are indicated. The author and his students have been most active in the study of salt absorption by the host plant through the mycorrhizal organ. These studies are described in detail.

In considering the ecology of ectotrophic mycorrhizae the author summarizes the laboratory work on these structures and suggests ways in which the concepts so obtained can be applied to a field condition. The fact that trees with definite mycorrhizal associations are better able to survive conditions which would otherwise result in poor growth does not help to explain the nature of the relationship. The effect of light, oxygen supply, nutrients, pH and other factors of the environment, as well as the effect of one fungal partner or another under specific field conditions, still need exploration in the field. Until such experiments, as well as others, are carried out, any attempt to relate laboratory experiments with field observations will result merely in speculation.

Endotrophic mycorrhizae are as varied as the groups of plants with which they are associated. The two more important plant groups possessing such mycorrhizae are the Ericales and the Orchidaceae. Following a description of the mycorrhizae of the Ericales, and of the search for the fungi which have produced these structures, it is emphasized that too little is known about the phenomenon in this order to make a general statement on the value to the plant of the fungus, or vice versa.

General features of the mycorrhizae of the Orchidaceae are given as descriptions of the anatomy of the structure, the plant species with the better known mycorrhizae, and the significance to the plant of a partial or permanent saprophytic existence during which time it is presumably fed by the fungus. A number of fungi have been isolated from orchid mycorrhizae and some phases of the nutrition of these fungi have been studied. In spite of the fact that orchid seeds can be germinated in culture aseptically, in nature this process seems to be carried out in association with a fungus which lives with the seedling for a time, or, if the plant is saprophytic, throughout its life. Concerning the biology of this type of mycorrhiza the student can only speculate at the present time.

Other plants are mycotrophic. Of those with septate endophytes, some of which have been isolated and partially studied in pure culture, are species of Gentianaceae, and some saprophytes such as the Bryophytes *Aneura, Cryptothallus,* members of the Burmanniaceae, the Triuridiaceae, the prothalli of sporophytes and gametophytes of *Psilotum.* In addition certain Bryophytes, two species of *Lobelia,* and members of the Cistaceae are known to be infected with septate hyphae in a mycorrhiza-like growth.

Certain plants are infected in mycorrhiza-like associations with aseptate mycelium attributed to certain Phycomycetes including species of *Endogone* which produces truffle-like fruit-bodies. These types of infection are described in general, and specifically for *Taxus,* certain Leguminosae, Gramineae, Bryophyta, Araliaceae and Cornaceae. Certain fossil records of *Rhizophagus*-like organisms associated with *Rhynia* and other plants are described.

While the first part of the book presents an account of recent studies and our accumulated knowledge of ectotrophic mycorrhizae, the latter part of the book, on endotrophic mycorrhizae, is hardly more than a literature review. However, much more work has been done in the former area than in the latter, and such a result might therefore not be unexpected. The book is well written, well illustrated with photomicrographs, photographs and line drawings, and is concluded with a list of more than 450 references, a subject index and an author index. The binding could have been improved. It will be a worthwhile addition to ecological reference libraries wherever problems involving mycorrhizae occur; that is, everywhere.

[1] Harley, J. L., 1959. The biology of mycorrhiza. Plant Science Monographs (1), Leonard Hill, Limited, London, and Interscience Publishers, New York (1960). xiv + 233 pp., 10 pl., 34 tables, 15 text figs. 55 s., $8.75.

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Mycology of Soils and Waters

At the Stillwater meetings I was asked to list courses in which one could learn something of pollution mycology. This I could not do at the time. However, in addition to those books previously reviewed in these pages which deal with one or another aspect of the study of fungi, four may be cited which could aid in learning something about the fungi in aquatic habitats whether these be clean or polluted.

The first of these[1] describes all those species of simple fungi known to occur in water as of 1955. These fungi may be saprobic on dead organic matter of one kind

[1] Sparrow, Frederick K., Jr. 1960. Aquatic phycomycetes. Second revised edition. University of Michigan Press, Ann Arbor (Univ. Mich. Scient. Ser. Vol. XV) and Ambassador Books, Ltd., Toronto. xxv + 1187 pp., 89 fig., keys. $22.50.

or another, or they may be parasitic on various types of plankton or on pollen grains. In addition, citations to the more complex aquatic fungi are given together with species descriptions for species published since the appearance of the cited monographs. An extensive 60-page bibliography listing 1300 titles is given. For the systematic mycologist this is the definitive work on water molds or true aquatic fungi. To use it adequately for identification purposes, one should have studied for a semester with the author, one of his students or one of the mycologists in the country trained in aquatic fungi.

For the ecologist, this volume contains some interesting materials. Habitats and habits are given for each of the 10 orders considered. This information is given in detail in relation to the various stages in the life history of the organism, or in relation to its parasitic nature and its host relationships, usually with the introduction to the order, sometimes with the family or genus. Each species description includes certain habitat data of ecologic interest.

For the ecologist primarily concerned with limnology, who wishes to obtain a picture of the total population of his study area, who has no access to cooperation from a mycologist, and who has the courage to tackle this book separately or together with the keys provided by Dr. Sparrow in the second edition of Fresh Water Biology, this would be an excellent addition to the reference shelf.

The words "industrial mycology" in the title of the second offering[2] may be misleading, but the book is equally useful to the industrial, the applied, the soils, or any other mycologist. In it are described techniques of collecting materials for study, techniques of studying these materials, and techniques for identification of the fungal organisms found. Introductory materials cover such subject matter as the place of fungi among living things, basic classification and problems of nomenclature. More than half the book is taken up with the classification of different groups of those fungi most often found in soils, as laboratory contaminants, in medical materials and in industrial processes. Laboratory equipment and technique, culture media of all kinds, supplementary nutrients, types of culture and culture techniques, special biochemical study procedures, methods of isolation and purification of cultures, avoidance of contamination, and microscopic manipulation leading to identification are considered in sufficient detail so that the student may have little difficulty in studying samples. A chapter is devoted to the maintenance of a culture collection, keeping the cultures alive and free from contaminants, mites and other organisms. The study of physiology of fungi requires techniques which are described adequately. In some industrial processes mold growth must be controlled or prevented, other industrial processes require special types of mold growth for production of one type of chemical or another. Each of these subjects is given a special chapter. Finally one chapter is devoted to a survey of mycological literature, another to techniques of microscopy. As an aid in developing culture techniques and identifying the resulting molds, this is an excellent book to have available.

For the identification of soil fungi isolated from soil and water samples, at least to genus, the spiral bound, off-set printed book by Barnett[3] can be most helpful. In it are illustrated 462 genera of Fungi Imperfecti and those Phycomycetes with conidial states usually found separately from products of sexual fusion upon which classifications are usually based. This can be an excellent supplement to Smith's book.[2]

For those who have seen mold cultures, and for those who have tried to interpret wide series of mold cultures assigned to one species but which exhibit such variation that the ends of any of several series could be interpreted as separate species, Pontecorvo's analysis[4] should be helpful. The series of lectures on which this volume was based were designed to add to current genetic thought by recombining certain ideology through the use of materials derived from the study of fungi and bacteria among other organisms. For the mycologist who wishes to try to understand some of the variability found within one species, or for the ecologist who wishes to try to interpret the multitude of habitats in which a single organism can be found, the development of genetic theory leading up to the phenomena of mitotic recombination and parasexuality can be highly enlightening

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[2] Smith, George. 1960. An introduction to industrial mycology. Fifth edition. St. Martin's Press, New York. xvi + 399 pp., 168 figs. $10.00.

[3] Barnett. H. L. 1960. Illustrated genera of imperfect fungi. Second edition. Burgess Publishing Co., Minneapolis. iii + 225 pp., 462 figs. $4.50.

[4] Pontecorvo, G. 1958. Trends in genetic analysis. Columbia University Press, New York (Columbia Biol. Ser. XVIII). x + 145 pp. $4.00.

Evolution and Natural Selection[1]

These two books, originally published four years apart, are to a large extent complementary. The overlap which occurs is understandable since both authors are from the same stable.

The first few chapters of Dr. Cain's book are a masterly exposition of the methods and background of 'orthodox' taxonomy of animals. Perhaps the choice of examples could have been better. They do illustrate the points he is making, but they are often groups of animals from remote areas, and the paucity of illustrations, presumably inevitable in an inexpensive book, means that one is not easily able to visualize the animals from the descriptions. However this is a minor complaint, and one would have to go a long way for such a clear introduction to the subject. If only such a good account were available for plant taxonomy!

The real meat of the book is contained in the following three chapters, on "the biological species" "Other sorts of species" and "Geographical speciation." Here Cain moves away from the classical taxonomists' ideas of species, or

[1] Cain, A. J. 1960. Animal species and their evolution. Harper & Bros., New York (Harper Torchbooks 519). 190 pp., 5 figs. Paperbound, $1.35. (First edition Hutchinson & Co., Ltd., London, 1954).

Sheppard, P. M. 1960. Natural selection and heredity. Harper & Bros. New York (Harper Torchbooks 528). 209 pp., 8 figs. Paperbound, $1.35. (First edition Hutchinson & Co. Ltd., London, 1958).

morphospecies, as he calls them. These, based on type specimens, are invaluable as a basis for the present day biologist, but the development of our ideas on species in recent decades has rendered many of them out of date. Unfortunately, too many biologists do not go beyond the stage of classifying, whereas such classification should merely be the first stage, preceding more detailed biological work.

It is with the more recent ideas of species formation, the biological criteria that are used to distinguish species, and the impact they have had on classical taxonomy, that these later chapters deal, and this account of modern trends is as lucid as the first part of the book. Certainly the reader with little or no previous knowledge of the subject should be able to understand the ideas presented without much difficulty.

Dr. Cain is no mean botanist, and this fact makes it regrettable that he did not widen the scope of his account to include more examples from the plant world into the discussion on speciation; they would have provided stronger backing for some of his views. Unfortunately when plants are mentioned in his discussion of polyploidy he does not make at all clear the relative importance of auto- and allo-polyploidy. There is no clear dividing line between them, and there are no doubt all stages between the two types of polyploidy in nature. It is rather an understatement to say of allotetraploids, however, "their formation in plants in the wild and under cultivation has been detected, and in at least one case a good species, found in the wild, has been synthesized from its parent forms."

Dr. Sheppard has brought more botanical examples into his account of natural selection and heredity, and on the topic of polyploidy is more accurate. This book is an excellent account of the basic principles underlying natural selection, a particularly difficult task in view of the amount of evidence to be considered. Sheppard himself admits that a book ten times the size would be needed to cover the subject comprehensively. It does seem that in an attempt to interest a wide audience, the author has spent too much of his space on elementary principles, but not enough to enable the non-biologist to grasp some of the ideas presented later on. The average student with a basic grounding in genetics should find the book invaluable, however, and he can skip the first three chapters. It is always a problem to write a book that satisfactorily caters for the advanced student and for the intelligent layman, and one wonders if it is better not to try, but to write one for each.

The chapters on polymorphism, stable polymorphism, polygenic inheritance, recombination, mutation and genetic drift, and the evolution of dominance constitute the most important and the best written part of the book. If the examples chosen are mainly from two groups, the Lepidoptera and the Mollusca, this is a reflection of the relatively large amount of work carried out in these groups on natural selection in action rather than one of personal bias on the part of the author. Both he and Cain have collaborated with E. B. Ford, who with his group at Oxford has been studying the problems for many years, and it is a measure of the vigour of the group that two such stimulating books have come from its members recently.

If these books can be faulted in one particular, it is in their failure to consider genetic systems as a whole; it is on these that natural selection exerts its pressures. Sheppard excuses himself from the omission on the grounds of lack of space and the existence of C. D. Darlington's brilliant book THE EVOLUTION OF GENETIC SYSTEMS. Perhaps it would have been better to have utilized the space given to elementary Mendelism for this purpose, and to have referred the reader to an elementary genetics text for the background.

I do not want to discourage anyone from reading these inexpensive books for this reason, however. They are both well worthy of study by every biologist, whatever his main interests.

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TIDES[1]

This book presents an elementary account of the phenomena of the tides, written by one of the leading oceanographers of Europe. Because of the precision with which the forces which produce the tides are known from astronomical considerations, the study of tidal phenomena has provided one of the most beautiful chapters of geophysics and the prediction of the tides in coastal waters is among its most satisfactory achievements. For the same reason, however, even the elementary account of the subject is usually presented in mathematical language which conceals the interest from the popular reader. Professor Defant has succeeded in giving an account of the principal phenomena of the tides, of the techniques employed in their observation and of the ideas which govern their analysis, which is clear, accurate and authoritative, without resort to more than one simple equation.

The author's personal investigations have been concerned with the modifications of tidal motions as influenced by the boundaries of enclosing basins. The longest chapter, on "The tides of the Seas and Oceans," is particularly welcome in treating this matter in greater detail than can be obtained from other popular accounts of the tide. The concluding chapters on "Tidal Oscillations in the Atmosphere and in the Ionosphere" and in "Tides on Land" will interest those already familiar with the ocean tides, but unacquainted with these other manifestations of the tide-generating forces.

The book is a translation of one published in Germany in 1953. The University of Michigan Press should be thanked for making it availale to American readers.

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[1] Defant, Albert. 1958. Ebb and flow; the tides of earth, air, and water. (Translated by A. J. Pomerans from the German, 1953, Springer-Verlag, Berlin). University of Michigan Press, Ann Arbor (Ann Arbor Science Paperbacks 506). 121 pp., 64 figs., 8 tables. $1.95.

New Serials

First issues of a new ecological journal, the Bulletin of the International Society for Tropical Ecology, have been received by the review editor. The Society is an outgrowth of discussions in international meetings at Dehra Dun in 1954, Kandy in 1956, and Bogor in 1958, at which the need for active research in tropical ecology and for a society supporting and encouraging such research was recognized. The Society was organized under the leadership of Indian ecologists—J. C. Sen Gupta of Calcutta is now president, and G. S. Puri of Allahabad general secretary—but is international in objectives and membership. In North America F. R. Fosberg, Washington, is a vice president, and P. Dansereau, Montreal, and T. Gill, Washington, are representatives from national committees for the Society. Membership of all ecologists interested in the tropics is welcome, and submission of papers from all countries to the Bulletin is invited. Inquiries regarding membership (Rs. 20/–, $4.75) may be addressed to Dr. F. R. Fosberg, Pacific Vegetation Project, % National Research Council, Washington 25, D. C. The first volume of the Bulletin, for 1960, includes messages to the new Society, and an international Forest Ecosystem Symposium of papers prepared for the International Botanical Congress in Montreal.

The first number has been received also of a new international journal of general biology, the Journal of Theoretical Biology. The Journal is intended as a central publishing medium for theoretical work in all fields of biology, to make possible publication of theoretical papers of general interest which are often unwelcomed by journals directed toward publication of experimental results. The first issue, for January 1961, includes along with a number of papers on theory in molecular biology, "An analysis of the idea of 'resources' in animal ecology" by H. G. Andrewartha and T. O. Browning. Chief editor is J. F. Danielli, Zoology Department, Kings College, Strand, London W.C.2. The Journal is published by Academic Press Inc., and subscriptions (86s., $12.00 for private individuals) should be sent to that firm at 17 Old Queen St., London S.W.1, or 11 Fifth Ave., New York 3.

An event of interest also is the appearance of a new series of books, the Flora et Vegetatio Mundi, with the first volumes by Hultén and Oberdorfer below. Additional volumes on vegetation are to be published, and works on the Middle East by Zohary, on Greenland by Böcher, on Peru by Ellenberg, and on the Congo by Lebrun are to appear in the near future. The series, edited by Reinhold Tüxen, is published by J. Cramer, P. O. Box 166, Weinheim/Bergstr., Germany. The firm of Cramer is successor to H. R. Engelmann, Leipzig; and the new series represents a revival in somewhat different form of the notable volumes of Die Vegetation der Erde, edited by Engler and Drude. Some volumes of the earlier series—Harshberger's Phytogeographic survey of North America ($21.00), Cockayne's Vegetation of New Zealand ($21.00), and Graebner's Die Heide Norddeutschlands ($5.50) are still available through Cramer, along with a reprinting of Schimper's Plant geography upon a physiological basis ($42.00).

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BOOKS AND MONOGRAPHS RECEIVED FOR REVIEW

Abbott, R. Tucker. 1961. How to know the American marine shells. New American Library, New York (Signet Key Book). 222 pp., 148 figs., 12 color plates. Paperbound $0.75.

Andrews, Henry N., Jr. 1961. Studies in paleobotany. John Wiley & Sons, Inc., New York & London. xii + 487 pp., figs.

Asimov, Isaac. 1961. The wellsprings of life. New American Library, New York (Mentor Book). 200 pp. Paperbound $0.50.

Bates, Marston. 1961. The forest and the sea; a look at the economy of nature and the ecology of man. New American Library, New York (Mentor Book). 216 pp. Paperbound $0.50.

Bates, Marston. 1961. Man in nature. Prentice-Hall, Inc., Englewood Cliffs, N. J. (Foundations of Modern Biology Series). xi + 116 pp., 35 figs. Paper $1.50, cloth $2.95.

*__Becker, Herman F.__ 1961. Oligocene plants from the upper Ruby River Basin, southwestern Montana. Geological Society of America Memoir **82**, 127 pp., 32 plates.

Bertalanffy, Ludwig von & Anatol Rapoport, editors. 1960. General Systems; Yearbook of the Society of General Systems Research, Vol. V, 1960. Society of General Systems Research, 205 N. Forest Ave., Ann Arbor, Mich. xvii + 235 pp. $7.50.

Braun, Werner, editor. 1960. Biochemical aspects of microbial pathogenicity. (symposium) Annals of the New York Academy of Sciences, Vol. **88**, Art. 5, pp. 1021-1318. $5.00.

Brewer, Richard. 1960. A brief history of ecology. Part I—Pre-nineteenth century to 1919. Occasional Papers of the C. C. Adams Center for Ecological Studies (Western Michigan University, Kalamazoo), No. 1, 18 pp.

Brown, Vinson & Henry G. Weston, Jr. 1961. Handbook of California birds. Naturegraph Co., 8339 W. Dry Creek Rd., Healdsburg, Calif. iv + 156 pp., num. figs., 8 color plates. Paper $2.95, cloth $4.50.

Burns, J. J., editor. 1961. Vitamin C. (symposium) Annals of the New York Academy of Sciences, Vol. **92**, Art. 1, pp. 1-332.

Curry-Lindahl, Kai. (1961). Sarek. Raben & Sjögren, Stockholm (Sveriges Nationalparker IV). 56 pp., figs. 3:—

Carrington, Richard. 1961. A guide to earth history. New American Library, New York (Mentor Book). 284 pp., 42 figs. Paperbound $0.75.

Chandler, Asa C. & Clark P. Read. 1961. Introduction to parasitology, with special reference to the parasites of man. 10th edn. John Wiley & Sons, Inc., New York & London. xii + 822 pp., 258 figs. $9.75.

Cronquist, Arthur. 1961. Introductory botany. Harper & Bros., New York. ix + 892 pp., figs. $9.25.

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*Assigned for review.

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